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# The environmental change in coastal ecosystems during the Late Holocene as recorded in seagrass sedimentary archives

## El cambio ambiental en ecosistemas costeros durante el Holoceno reciente según el archivo sedimentario de las fanerógamas marinas

Carmen Leiva Dueñas

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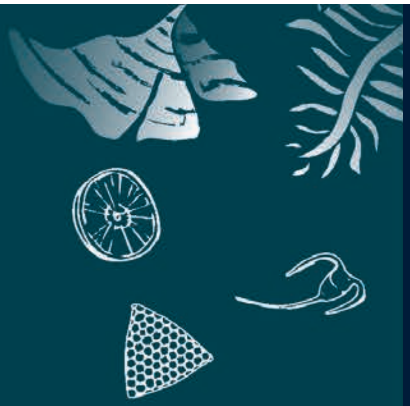

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Carmen Leiva Dueñas · 2020 ·

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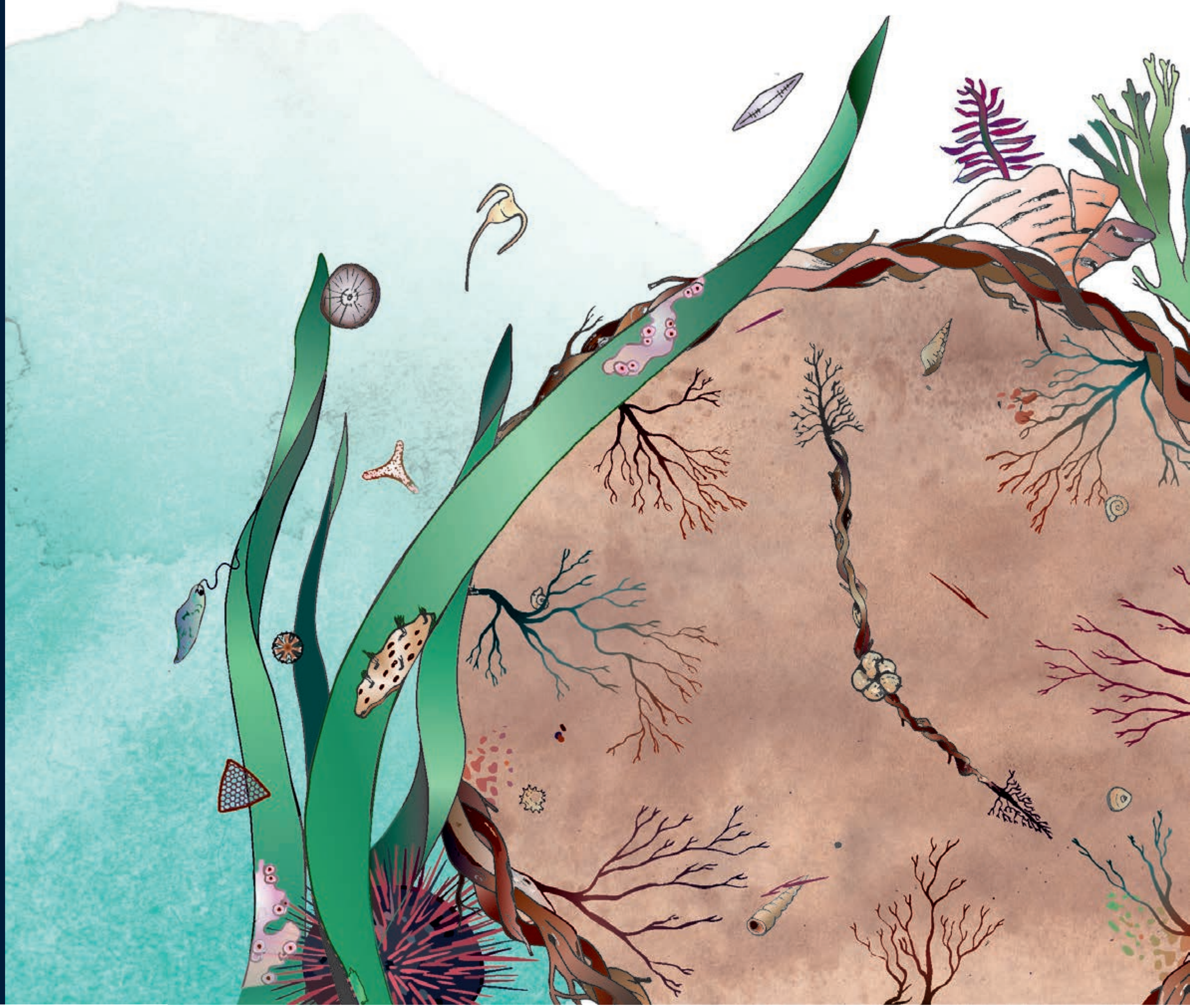

UNIVERSITAT DE BARCELONA

Departamento de Biología Evolutiva, Ecología y Ciencias Ambientales
Programa de Doctorado en Ecología, Ciencias Ambientales y Fisiología Vegetal

# The environmental change in coastal ecosystems during the Late Holocene as recorded in seagrass sedimentary archives

Memoria presentada por Carmen Leiva Dueñas para optar
al Grado de Doctora por la Universidad de Barcelona

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Centro de Estudios Avanzados de Blanes (CEAB-CSIC)
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*A mi familia.*

*Dejé la estepa*
*cansado y aturdido;*
*pasto de la ansiedad*
*no hay otros mundos*
*pero si hay otros ojos,*
*aguas tranquilas,*
*en las que fondear.*
*Mar antiguo, madre salvaje,*
*de abrigo incierto que acuna el olivar.*
*muge mi alma, confusa y triste;*
*ojos azules en los que naufragar.*
*Te he echado tanto de menos*
*patria pequeña y fugaz;*
*que al llegar cruel del norte el huracán*
*no se apague en tu puerto el hogar.*
*Mar antiguo, madre salvaje,*
*en tus orillas de rodillas rezaré.*
*tierra absurda que me hizo absurdo,*
*nostalgia de un futuro azul en el que anclar.*
*Triste y cansado, con los viejos amigos*
*el vino y el cantar;*
*mientras quede un olivo en el olivar*
*y una vela latina en el mar.*
*Viejos dioses olvidados*
*mantenednos libres de todo mal.*
*Mar antiguo, dios salvaje*
*de la encina y del gris olivar.*

"Mar antiguo" (El último de la Fila).

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# ADVISORS' REPORT

Dr. Miguel Ángel Mateo, research scientist at the Center for Advanced Studies of Blanes (CEAB), and Dr. Antonio Martínez Cortizas, professor at the Department of Edafology and Agricultural Chemistry (University of Santiago de Compostela), as advisors of the PhD thesis entitled "The environmental change in coastal ecosystems during the Late Holocene as recorded in seagrass sedimentary archives",

INFORM that the research developed by Carmen Leiva Dueñas for her Doctoral Thesis has been organized in four chapters, which correspond to four scientific papers listed below, three published in scientific journals (their impact factors and quartiles are included) and one currently prepared as a manuscript to be submitted in the next months; including a General Introduction and a General Discussion with Conclusions;

and CERTIFY, that the research has been carried out by Carmen Leiva Dueñas, participating actively in all the tasks: setting the objectives, conceiving and performing the analyses, participating actively in the field and laboratory work, handling and analyzing the results, and writing the manuscripts.

Finally, we certify that the co-authors of the publications listed below that are part of this doctoral thesis, will not use them as part of any other national or international Doctoral Thesis.

Blanes, 17th November 2020

Dr. Miguel Ángel Mateo

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In addition, the results of this thesis have been presented at international and national conferences: International ASLO, Hawaii Convention Center, Honolulu, USA, 2017; VI International Symposium on Marine Sciences, Vigo, Galicia, Spain, 2018; International ASLO, San Juan, Puerto Rico, USA, 2019; 20th Congress of the International Union for Quaternary Research, Dublin, Ireland, 2019.

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# CONTENTS

# SUMMARY

Coastal ecosystems, especially the vegetated areas, are among the most threatened ecosystems in the world, undergoing a fast and constant decline. Their losses are of serious concern due to their elevated production, providing many ecosystem services essential to the well-being of our societies. Behind the regressive trends of the coastal ecosystems, there is a plethora of adverse human pressures, going from local and regional impacts, including anthropogenic activities in and outside the coastal regions, to large-scale drivers of change, such as the global warming. Nevertheless, there is a critical lack of long-term information about the vegetated coastal ecosystems, information that can provide baseline ecological data of their natural dynamics and vulnerability.

Seagrasses are marine plants, engineering species that form underwater meadows, which, among many other services, provide essential habitat for many other organisms. Seagrasses meadows are experiencing a widespread decline since the early 20th century. This regression is accelerated for the Mediterranean endemic seagrass species *Posidonia oceanica*. Long-term studies are of particular interest in *P. oceanica* meadows because this species is a large-slow growing and long-lived seagrass, which substantial changes and responses manifest over time scales of decades to centuries. A deeper understanding of seagrass long-term dynamics can help managers to apply meadow-specific actions and act at the appropriate temporal scales. The discipline of paleoecology allows the study of long-term ecosystem dynamics on time scales of centuries to millennia, and it can be used in seagrass meadows thanks to the organic deposits accumulated below *P. oceanica* meadows. Paleoreconstructions using seagrass deposits are still scarce and have mainly focused on allogenic (externally controlled) processes.

In this dissertation, a paleoecological approach at a regional spatial-scale was used to explore the long-term dynamics of the autogenic and biotic ecological components of Mediterranean seagrass meadows, mainly *P. oceanica* meadows. Initially, we investigated the

usefulness of several biogeochemical proxies and a technique (FTIR-ATR spectroscopy) so far unexplored in seagrass deposits, as well as which were the main biogeochemical processes recorded by them. We described the long-term dynamics of the seagrass ecosystem, the main drivers of change, and their relative importance. The results indicated that seagrass long-term dynamics are oscillating. Even though most meadows showed regressive trends during the last 150 years, seagrass trends varied spatially, with the main spatial differences occurring at the inter-regional level. Differences in long-term dynamics between local sites seemed mostly dependent on the environmental background of each site, which also affected seagrass long-term resilience. The major factors responsible for long-term variability of seagrass ecosystem dynamics were multiple and at both, local and large spatial scales. However, the balance between the contribution of local and large-scale drivers varied spatially. The influence of climate seemed especially crucial in meadows surrounded by more turbid waters, under the influence of higher fluvial discharges. These meadows showed lower long-term ecosystemic resilience.

In summary, this research showed that seagrass long-term dynamics can be studied through their paleoecological record, providing a valuable frame of reference for evaluating the magnitude of current changes and consequences of combined diverse impacts on these marine ecosystems. The results of this thesis indicated that despite some spatial variability of the long-term dynamics, the major changes occurred over the last century, predominating trends of seagrass decline or community compositional changes. Moreover, our results point to a more acute negative impact of present climate change in meadows where light availability is compromised due to local factors. The overall spatial variability regarding seagrass long-term dynamics highlights the need for meadow-specific local management with background information, information that can be obtained from paleoecological studies.

# RESUMEN

Los ecosistemas costeros, especialmente aquellos dominados por macrófitos sumergidos o semi-sumergidos, se encuentran entre los ecosistemas más amenazados del mundo, sufriendo un rápido y constante declive. Sus pérdidas son motivo de grave preocupación debido a su elevada producción, y a que proporcionan muchos servicios ecosistémicos esenciales para el bienestar de nuestras sociedades. Detrás de las tendencias regresivas de los ecosistemas costeros, se encuentra una plétora de presiones humanas adversas, que van desde impactos locales y regionales, incluidas actividades antropogénicas dentro y fuera de las regiones costeras, hasta agentes de cambio a gran escala, como el calentamiento global. Sin embargo, existe una falta crítica sobre el cambio a largo plazo de los ecosistemas costeros vegetados, información que puede proporcionar datos ecológicos de referencia sobre sus dinámicas naturales y vulnerabilidad.

Las fanerógamas marinas son plantas superiores creadoras de estructuras tridimensionales complejas que, entre otros muchos servicios, dan lugar a un hábitat de elevada biodiversidad. Estos macrófitos están experimentando un declive generalizado desde principios del siglo XX, regresión especialmente acelerada para la especie endémica mediterránea, *Posidonia oceanica*. Los estudios a largo plazo son de particular interés en las praderas de *P. oceánica*, pues al ser una planta marina de gran tamaño, de crecimiento lento y de vida larga, sus cambios y respuestas sustanciales se manifiestan en escalas de tiempo de décadas a siglos. Una comprensión más profunda de la dinámica a largo plazo de las fanerógamas marinas puede ayudar a los gestores a aplicar acciones específicas y actuar en las escalas temporales adecuadas. La disciplina de la paleoecología permite el estudio de la dinámica de los ecosistemas a largo plazo en escalas de tiempo de siglos a milenios, y se puede aplicar en praderas de fanerógamas de *P. oceanica* gracias a los depósitos orgánicos acumulados bajo ellas. Las reconstrucciones paleoecológicas que usan suelos de praderas marinas aún son escasas y las que hay se han centrado principalmente en procesos alogénicos del ecosistema (controlados externamente).

En esta tesis se ha hecho uso de reconstrucciones paleoecológicas en praderas de fanerógamas mediterráneas, principalmente de *P. oceánica*, a una escala espacial regional con el objetivo de explorar la dinámica a largo plazo de los componentes ecológicos autogénicos y bióticos. Inicialmente, se investigó la utilidad de varios *proxies* (indicadores) biogeoquímicos y de una técnica (espectroscopía FTIR-ATR) hasta ahora inexplorados en depósitos de praderas marinas, así como cuáles eran los principales procesos biogeoquímicos registrados por estos depósitos. Los resultados obtenidos permitieron describir la dinámica a largo plazo de las praderas marinas, así como sus principales impulsores del cambio a largo plazo y su importancia relativa. Se observó que la dinámica a largo plazo es oscilante, y que la mayoría de las praderas mostraban tendencias regresivas durante los últimos 150 años. Sin embargo, estas tendencias de declive variaban espacialmente, ocurriendo las principales diferencias a escala interregional. Las diferencias en la dinámica a largo plazo entre localidades parecían depender principalmente del contexto ambiental de cada sitio, lo que también afectaba a la resiliencia a largo plazo de las praderas. Los resultados revelan que los principales factores responsables de la variabilidad a largo plazo son múltiples, incluyendo factores de carácter local pero también regional y global. Sin embargo, la contribución relativa entre los factores de influencia local y de gran escala varia espacialmente. La influencia del clima parece especialmente crucial en praderas creciendo en aguas más turbias, bajo la influencia de descargas fluviales más abundantes. Estas praderas mostraron una menor resiliencia ecosistémica a largo plazo.

En resumen, esta investigación ha demostrado que las dinámicas a largo plazo de las fanerógamas marinas se pueden estudiar a través de su registro paleoecológico, proporcionando un valioso marco de referencia para evaluar la magnitud de cambios actuales y las consecuencias de diversos impactos combinados en estos ecosistemas marinos. Los resultados de esta tesis revelan que, a pesar de cierta variabilidad espacial de las dinámicas a largo plazo, los cambios más importantes han ocurrido durante el último siglo, predominando las tendencias de declive de la fanerógama o cambios en la composición de las comunidades que alberga. Además, nuestros resultados apuntan a un impacto negativo más agudo del actual cambio climático en aquellas praderas donde la disponibilidad de luz se ve comprometida debido a causas locales. La variabilidad espacial general de las dinámicas a largo plazo de las praderas marinas destaca la necesidad de una gestión local específica a cada pradera, con información previa contextual, información que se puede obtener a partir de estudios paleoecológicos.

# GENERAL INTRODUCTION

# 1. SEAGRASS ECOSYSTEMS

## 1.1. Generalities and Mediterranean seagrass meadows

Seagrasses are the only flowering plants found in the marine environment. They can form lush, extensive and highly productive underwater meadows along the coast of all continents except Antarctica (Green & Short, 2003). Seagrasses constitute a functional group, with 72 species identified around the world and ten of them at high risk of extinction (Sculthorpe, 1967; Short et al., 2011). The two main species distributed along the Mediterranean Sea are *Cymodocea nodosa* (Ucria) Ascherson and *Posidonia oceanica* (L) Delile, the latter being the most abundant and endemic to this sea. *P. oceanica* meadows are one of the most relevant coastal habitats considering their abundance, extension and ecological value. They are considered equivalent to forests in terrestrial ecosystems (Ruiz Fernandez et al., 2009; Telesca et al., 2015).

Seagrasses have a crucial role in the coastal communities providing multiple invaluable ecosystem services (Costanza et al., 1997). They constitute biodiversity hotspots by being essential habitat and nursery ground for many fishes and invertebrates (Heck et al., 2003; Gillanders, 2006). In fact, seagrasses are considered engineering species, meaning that they create most of the structure of the community and «modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials» (Jones et al., 1994). Consequently, the decline and loss of seagrass species adversely affect many other organisms, profoundly affecting the whole coastal community (e.g. Thomson et al., 2015; Zhang & Silliman, 2019). Seagrasses canopies slow down water currents and cause the deposition of suspended particles, which clears coastal waters and improves their quality (Gacia & Duarte, 2001; Lacy & Wyllie-Echeverria, 2011; Vassallo et al., 2013; Fonseca et al., 2019). Their high primary productivity supports diverse marine food webs and contributes significantly to carbon burial in seagrass sediments (Kennedy et al., 2010; Fourqurean et al., 2012). Their developed belowground organs can even stabilize the seabed, which helps to reduce shoreline erosion (Duarte, 2002; Spalding et al., 2003; Orth et al., 2006a).

Their habitats are primarily characterized by very high light availability (Zimmerman, 2006) and minimum levels of current velocity and wave energy, both closely related with the sediment characteristics and substrate stability they need (Fonseca & Bell, 1998; Koch et al., 2006). Seagrasses also require optimum salinity, temperature, and water and sediment nutrient availability (Hemminga & Duarte, 2000; Lee et al., 2007). There are complex interactions between all these environmental variables, which make very difficult to predict the ecosystem response to multiple disturbances (Eklöf et al., 2009; Collier et al., 2016; Ontoria et al., 2019a, 2019b).

## 1.2. Seagrass ecosystem dynamics

Seagrass meadows constitute highly dynamic ecosystems responding to natural and, more currently, anthropogenic environmental changes across a range of scales (Fig. 1) (Duarte et al., 2006; Rasheed & Unsworth, 2011; Unsworth et al., 2012; O'Brien et al., 2018a). Changes in seagrass meadows are ultimately the result of cumulative, small, fast processes (molecular to cellular scales) upscaling to plant-level responses that control the recruitment of new clones together with the growth and turnover of shoots (Duarte et al., 2006; O'Brien et al., 2018a). Seagrasses are clonal plants, hence, shoot recruitment, the addition of new individuals, is mostly by vegetative reproduction, and primarily through the spread of rhizomes, their stems. Shoot recruitment shows variable rates in time and space influenced by resources availability, but overall they are very low and meadows can take centuries to form (Kendrick et al., 2005; Sintes et al., 2006).

Given the lack of consensus (Borics et al., 2013), the terms disturbance and stressor will be used as synonyms in this thesis, defined as any factor (temporary or not) adversely affecting community structure and dynamics and preventing the ecosystem from reaching an ecological equilibrium and their maximum potential. Disturbances can be either natural (variations of incident solar radiation, extreme climatic events, diseases, grazing and bioturbation) or anthropogenic, as well as local or global, depending on their spatial extent. A meadow is stable if disturbances do not have a significant impact, which means it has reached a steady state in which the shoot recruitment is balanced with the shoot mortality (Duarte et al., 2006). However, if disturbances are substantial and overpass the seagrass resilience threshold (i.e. its resistance to the stressor and recovery from the degradation, Unsworth et al., 2015), the seagrass meadow is no longer stable. It will suffer changes in shoot density and biomass production that can extend at larger spatial and longer temporal scales. Seagrass decline is usually a gradual process, with a progressive loss of shoots. To prevent losses on larger scales, it is essential to detect the seagrass decrease as early as possible (Marbà, 2009).

Changes in seagrass abundance will be visible at longer time scales under the influence of intense and persistent disturbances. The seagrass species, the present and past condition of the meadow, together with the occurrence of negative feedback effects, do also play a role in the seagrass resilience (Kilminster et al., 2015; Maxwell et al., 2016; O'Brien et al., 2018b). Additionally, the time of response of seagrass ecosystems during degradation and recovery may differ with recovery times being longer. This happens because seagrasses ecosystems can also display hysteresis, i.e., non-linear trajectories which cause a change in state, and in which reinforcing feedbacks prevent recovery (Koch et al., 2009; Duarte et al., 2015; Maxwell et al., 2016). As mentioned above, the capacity of overcoming disturbances differs among seagrass species so that we can expect different temporal dynamics for different species. We can broadly differentiate seagrasses based on their ecological strategies and ability to recover from disturbances: colonizing, climax and opportunistic species. Small-fast-growing, with low physiological resistance but significant ability to recover after disturbances are colonizing seagrasses (e.g. *Zostera spp*.). Large-slow-growing, long-lived species, with high physiological resistance but that need more time to recover are persistent or climax species (e.g. *P. oceanica*). Their species-specific traits in vegetative growth and seedlings recruitment play a key role in the characteristic recovery time of each species (Orth et al., 2006b). *P. oceanica* typically requires decades to centuries to recover after disturbance (González-Correa et al., 2005; Walker et al., 2006). There are also species with mixed ecological traits, which are considered opportunistic (e.g. *Cymodocea spp*.; Duarte, 1991; Duarte et al., 1997; Kilminster et al., 2015; Roca et al., 2016). Seagrasses can form two main types of meadows according to their persistence over time: enduring and transitory meadows. Meadows that do not disappear are persistent, while those that go through periods of absence and presence are temporary. Transitory meadows are only formed by colonizing, opportunistic species, whose recovery is possible mainly due to a higher seed bank in the sediments (Orth et al., 2006b), while enduring meadows can derive from any seagrass. Transitory meadows can display their drastic changes beyond annual cycles and are more common in areas with widely fluctuating environmental conditions or where seagrasses are close to their distribution limits (e.g. deep waters; Kilminster et al., 2015).

The temporal variability of seagrass biomass or production has been most commonly studied at intra-annual scale. Over a year, seagrass variability shows a marked seasonality due to changes in light, temperature but also nutrient availability (e.g. Alcoverro et al., 1995, 1997; Gobert et al., 2002). Inter-annual variability in seagrass meadows can be high as a result of the interplay of a wide range of causes: natural processes, such as grazing and natural climate variability, local human activities deteriorating water quality and shoreline erosion, or the current fast global environmental change (McKenzie, 1994; Rasheed & Unsworth, 2011; Unsworth et al., 2012). The processes controlling the ecosystemic changes can be classified in allogenic or autogenic, and so are also the recorded sedimentary processes. Allogenic processes are external factors operating at broader spatial scales (basin, regional or global scale). Examples of allogenic processes affecting seagrass meadows are soil erosion and fluvial discharges, human-induced changes, the regional climate or the solar influence. In contrast, autogenic processes are local and inherent of the system. Hence, in seagrass meadows, autogenic processes are mostly biotic-induced. All of these processes ultimately affect and regulate resources availability (temperature, light, nutrients) to the seagrass (Duarte et al., 2006).

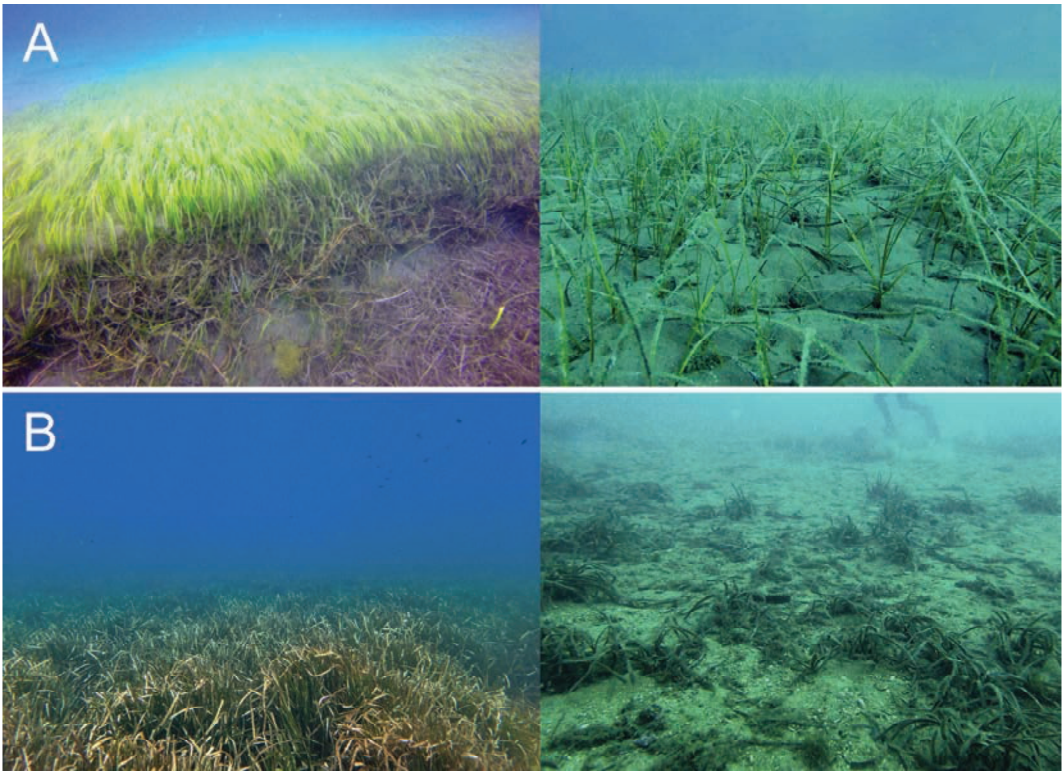

**Figure 1.** Photographs showing different seagrass meadows along the Andalusian coast, specifically in Almeria, which illustrates how dynamic these ecosystems can be. A) On the left, a healthy and dense *Cymodocea nodosa* meadow, located in Bajos de Alquián and, on the right, a sparse meadow of the same species in Palomares. B) On the left, a healthy and dense *P. oceanica* meadow in Aguamarga while, on the right, a degraded and sparse *P. oceanica* meadow in Roquetas.

### 1.3. Current trajectories and future scenarios

Multiple anthropogenic disturbances currently blur natural seagrass dynamics. Several studies about seagrass trends reported first recorded seagrass losses around the 1850-1870s and a widespread decline of most seagrass species since the 20th century. A decline widely accepted to be mainly due to anthropogenic causes, both of local and global magnitude (Orth et al., 2006a; Waycott et al., 2009; Short et al., 2011; Marbà et al., 2014). Over the last decades, the accelerating rate of seagrass decline has slowed down for most species in Europe, associated with conservation and protection measures at local and regional scales. However, recovery was only observed in some locations for fast-growing species (de los Santos et al., 2019).

For *P.oceanica,* the estimated decrease in surface coverage is about 34% across the entire Mediterranean basin over the last 50 years (Telesca et al., 2015). Human stressors are considered the main factors behind the current losses of *P. oceanica*. Some of these human-derived stressors are widespread local disturbances, derived from an increase in tourism and massive urbanisation along the Mediterranean coast. One example of local disturbance is the reduced water clarity due to eutrophication or suspended sediments (caused by dredging, terrestrial run-off, filling or direct physical damage due to certain fishing practices). Other human impacts have a broader spatial extent, such as the spread of invasive species and rises in temperature and water level due to current climate change (Orth et al., 2006a; Boudouresque et al., 2009; Marbà et al., 2014). The release of greenhouse gases to the atmosphere from human activities, mostly based on the burning of fossil fuels, has caused a significant and progressive increase in global temperature since the beginning of the industrial revolution (second half of the 19th century). A rise predicted to continue if human societies prolong their dependency on fossil fuels. The temperature rise has caused multiple drastic environmental changes, such as the increase in frequency and duration of extreme weather events (droughts, floods, heat waves), seawater acidification, ocean warming, and sea level rise, amongst many others (IPCC, 2013). The Mediterranean Sea is an area of particular vulnerability to climate change due to its semi-enclosed nature, being already one of the fastest-warming regions and expected to be one of the most affected by global warming (Giorgi, 2006; Vargas-Yáñez et al., 2008; IPCC, 2013). Rising sea surface temperatures and more frequent heatwaves in the Mediterranean are greatly impacting *P. oceanica*, whose shoot mortality rates have experienced a three-fold increase due to current warming (Mayot et al., 2005; Díaz-Almela et al., 2009; Marbà & Duarte, 2010).

Some of the expected environmental changes in marine habitats could have a positive effect on seagrass growth and photosynthesis, such as the increased atmospheric $CO_2$ concentrations. $CO_2$ is a limiting factor for most macrophytes at current ocean inorganic carbon concentrations, so its rise would likely increase the inorganic carbon availability benefiting seagrass photosynthesis and growth (Invers et al., 2001; Mateo et al., 2010; Koch et al., 2013; Russell et al., 2013; Cox et al., 2015). However, positive effects derived from increased $CO_2$ concentrations are not being observed. Simultaneous environmental stressors, such as light availability and temperature, have been shown to counteract the positive effects (Hendriks et al., 2017; Collier et al., 2018). Water temperature strongly affects seagrass photosynthesis and respiration, a positive effect within the optimal temperature range but if the temperature goes beyond the thermal optima (unique to each species), the rising temperature can negatively impact seagrass energetic balance and growth (Lee et al., 2007; Olsen et al., 2012). Heatwaves have already been reported to lead to extensive seagrass losses (Thomson et al., 2015; Nowicki et al., 2017; Arias-Ortiz et al., 2018). The ocean warming and the increase of marine heatwaves are further associated with shifts in species' distribution, which can favour the expansion of more thermotolerance seagrass species such as *C. nodosa* (Olsen et al., 2012; Ontoria et al., 2018). Sea-level rise due to climate change will increase water depth leading to reduced light availability and hence, less suitable habitats for seagrasses (Saunders et al., 2013). Other climate change-related stressors, such as weather changes towards increased rainfall and flooding and more frequent and intense storms can also impact meadows by uprooting, burying plants and by decreasing light availability as a result of increased turbidity (Duarte, 2002; Guidetti et al., 2008).

However, the individual effects of each environmental variable, expected to change, do not merely sum up. The combined effect of multiple stressors can be additive, synergistic, or antagonistic (e.g. Crain et al., 2009). Ontoria et al. (2019b) actually observed worsened *P. oceanica* physiological parameters due to a synergistic interaction between warming and ammonium additions. Their results may indicate that global warming in seagrass meadows affected by eutrophication could have a higher negative impact. Sadly, the model developed by Jordà et al. (2012) predicts that *P. oceanica* declining trends due to seawater warming will be ineludible even if other local anthropogenic pressures are entirely mitigated. Removing local pressures would only delay the functional loss of the meadows. However, they considered local anthropogenic and warming impacts as additive, which means that local actions to mitigate impacts in seagrass meadows could delay even further the seagrass declining trends if having synergistic effects.

## 2. LONG-TERM STUDIES TO UNDERSTAND CHANGES IN SEAGRASS MEADOWS

Despite the promising news of recovery for fast-growing seagrasses in Europe, these results are based on data that do not usually extend beyond the past few decades. The design and implementation of efficient management and conservation plans require a deeper understanding of its long-term dynamics. That way, managers can apply meadow-specific actions and act at the appropriate temporal scales. The long-term scale is especially crucial for larger and long-lived species, as is the case of *P. oceanica*. The complexity of seagrass ecosystems also requires knowledge from multiple science areas to comprehend the interactions between drivers, processes and their influence. Research projects often focus on one or two isolated components of the ecosystem without assessing their combined actions. They rarely comprise information across multiple disciplines, which is essential to understand causal relationships. Paleoecology is a thriving and exceptional discipline that allows the study of long-term ecosystem dynamics on time scales of centuries to millennia. The paleoinformation is an integration of all the past forcings and feedbacks because paleorecords have incorporated all processes occurring in the ecosystem (Bradley & Alverson, 2003; Seddon et al., 2014a). Therefore, paleoecology can be an excellent tool to investigate the ecosystem responses in the past and real multi-stressor scenarios.

Predictions of seagrass future trajectories as affected by current climate change will not be completely reliable as long as part of their variability remains unknown. Paleorecords provide insights into how the ecosystems responded to past changes and allow for a deeper understanding of its variability during pre-anthropic times. Overall, this information can help to evaluate and comprehend present-day trends, discriminate between the influences of natural climate and anthropogenic disturbances, and improve our ability to predict future scenarios in a changing world (Willis et al., 2007; Davies & Bunting, 2010; Birks et al., 2012; Seddon et al., 2014b).

Fortunately, the sediments accumulated below some seagrass meadows, especially those of the *Posidonia* genus, can serve as paleoarchives (e.g. Mateo et al., 2002; López-Merino et al., 2017; Lafratta et al., 2018). These species form several meters thick deposits with a highly coherent chronological layering and with high temporal resolution (2-17 yr cm$^{-1}$) (Fig. 2A-C) (Mateo et al., 2002; Lo Iacono et al., 2008; Serrano et al., 2012; Serrano et al., 2016a). These environmental archives are composed mainly of large pools of organic matter accumulated over millennia. Organic matter that derives from the seagrass itself and organisms inhabiting the meadow (Fig. 2D) (Mateo et al., 1997; Papadimitriou et al., 2005; Mazarrasa et al., 2017a). All this organic matter mixes with an inorganic matrix comprising terrigenous and bioclastic material (Fig. 2A) (Gaglianone et al., 2017). The preservation of the organic matter and many other biotic and abiotic proxies is promoted by the prevailing anoxic conditions in these deposits, as well as to the chemical recalcitrance of the seagrass-derived organic matter (Mateo et al., 2006; Kaal et al., 2016, 2019; Piñeiro-Juncal et al., 2018). The Late Holocene (last 4250 years) is the period encompassed by most of the available studies (Mateo et al., 1997, 2002; Lo Iacono et al., 2008; López-Merino et al., 2017; Lafratta et al., 2018), but sediment sequences older than 8000 yrs have recently been described (Monnier et al., 2019). Relatively stable climate conditions were considered to be prevalent during the Holocene. However, rapid climate changes were reported to have occurred throughout it (Mayewski et al., 2004). One of them is the Little Ice Age (150-600 cal yr BP), characterized by cold and wetter conditions, also in the Iberian Peninsula (Nieto-Moreno, 2012; Oliva et al., 2018). This makes the late Holocene an interesting period in order to assess how these rapid climate changes could have influenced seagrass dynamics.

Paleoecological studies also have limitations that should be considered if meaningful and cautious inferences are to be made about past environments. The first and most apparent is that any paleoecological study must rely on records of proxies that should, ideally, be well preserved. The limitations of selective preservation, or reworking due to bioturbation in marine sediments, are the ones the paleoecologist must continuously be aware of any

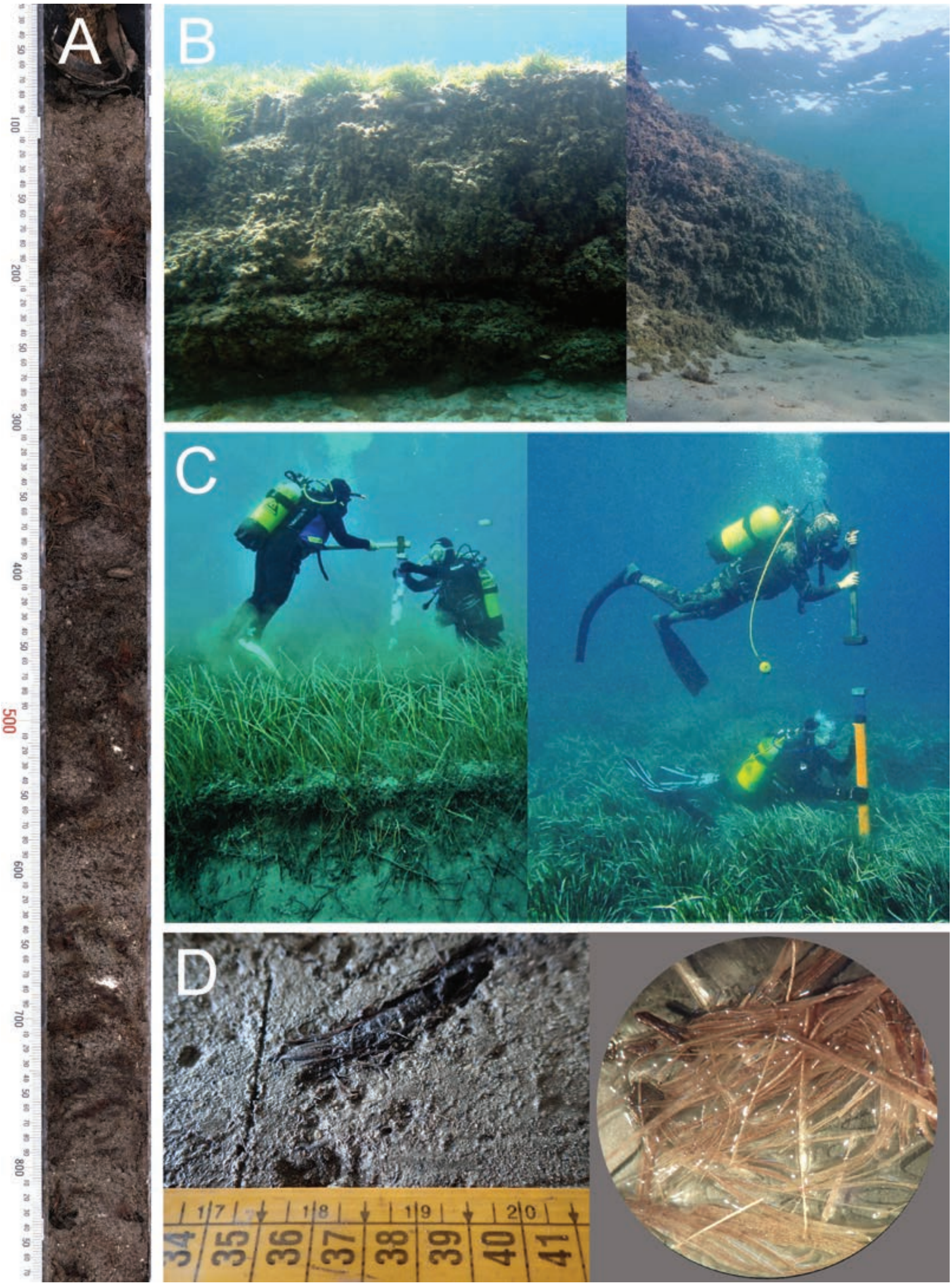

**Figure 2.** A) High-resolution picture of a core extracted from a *P. oceanica* organic deposit, note the higher amount of seagrass debris in darker areas. B) Erosional escarpments of the organic deposits accumulated under seagrass Posidonia meadows. C) Examples of coring over *P. oceanica* meadows along the Andalusian coast. D) Examples of seagrass debris found in the extracted cores; the picture on the left shows part of a very well preserved rhizome still within the sediment matrix, and the picture on the right are sheaths fibres picked from the organic deposits and observed under the stereomicroscope.

paleoenvironmental reconstruction relies to some extent on the premise that past environmental laws and processes can be interpreted based on what is currently known about them. This is the uniformitarian principle (Hutton, 1788). The uniformitarianism has practical and philosophical limitations. For example, it requires a present analogy for interpreting the past, and there can be former ecosystems and environments with no modern analogue. Relationships can also change over space and time. Moreover, reconstructing an initial condition from the end products (paleorecords) can be further complicated due to the nonlinear nature of many systems, which can have a stochastic behaviour not amenable to prediction. In other words, different environmental configurations can lead to similar proxy reactions, especially if we are using just a few proxies (Blaauw et al., 2010). Finally, multiple causal factors can interact and, for example, disentangling the relative importance of the climatic and anthropogenic signals can be a difficult task. In some cases, it can even be impossible. This is particularly the case for the mid- and late Holocene, when both climate and human impacts have been modulating the environment, interacting and mutually reinforcing their effects (Bell & Walker, 2005).

### 2.1. Paleoecological studies in seagrass ecosystems

The potential of the seagrass deposits as paleoarchives was initially acknowledged by Boudouresque et al. (1980) and Mateo et al. (2002, 1997). They revealed the chronological order of several *P. oceanica* deposits. From that moment on and before this thesis, the field of paleoecology in seagrass ecosystems has been gradually increasing. A wide range of proxies has been tested, allowing the reconstruction of different environmental changes. Examples include changes in terrestrial landscapes and land-use using pollen and glomalin-related soil protein analyses (López-Sáez et al., 2009; López-Merino et al., 2015, 2017); the reconstruction and impact of metal pollution on the coastal system through seagrass debris metal content (Serrano et al., 2011, 2013, 2016b, 2016c); stable carbon isotopes composition of seagrass debris allowed the reconstruction of millennial changes in seagrass production (Mateo et al., 2010); long-term dynamics of the sponge community through the quantification of sponge spicules (Bertolino et al., 2012); quantification of organic matter preservation using pyrolysis-GC-MS on the sediment organic matter (Kaal et al., 2016, 2019) and the impact of climatic factors, anthropogenic pressure and of seagrass loss and later revegetation in carbon burial (Macreadie et al., 2015; Marbà et al., 2015; Mazarrasa et al., 2017a, 2017b). Even archaeological remains have been discovered in *P. oceanica* deposits, preserved due to being embedded within the high anoxic sediments these deposits constitute (Votruba et al., 2016).

To get a realistic idea of the trends and priorities of using paleoecology in coastal ecosystems, I did a systematic review on Web of Science using the keywords and Boolean operators: (seagrass* OR "posidonia oceanica" OR "cymodocea" OR "thalassia" OR “zostera” OR "salt marsh*" OR "tidal marsh*" OR mangrove* OR estuar* OR “coral reef” OR "coastal lagoon*" OR “coastal wetland*” OR "coastal vegetated habitat") AND ("long-term ecology” OR “fossil pigment*” OR paleoecology OR paleoecology OR paleo-ecology OR paleo reconstruction OR palaeo-reconstruction OR “sediment record” OR palaeoenvironment OR paleoenvironment OR “paleo proxy"). I selected 278 references published since 1966 and found 28 relevant paleoecological studies in seagrass meadows and 250 in other coastal habitats (Fig. 3).

I classified the studies in two main groups, non-vegetated and vegetated coastal areas, the latter being also grouped into seagrass meadows, salt and tidal marshes, and mangroves. Even though the number of publications regarding paleoecology in coastal ecosystems is increasing every year, the number of paleoecological studies in vegetated ecosystems is lower than in non-vegetated areas, despite the ecological importance of the vegetated coastal ecosystems. Moreover, the comparison of the number of publications between seagrass and other vegetated coastal ecosystem shows significantly lower studies until very recently.

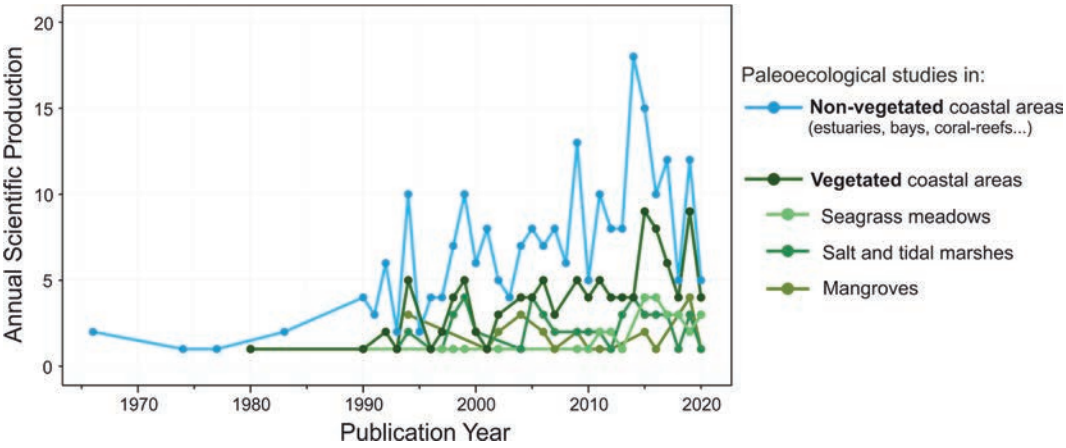

**Figure 3**. Number of papers on coastal paleoecology paleoecological papers in coastal areas published per year through searches in ‘web of science’ (WoS) according to different keywords (see text).

This delay in the increase of paleoecological studies in seagrass meadows likely translates into a gap in the current paleoecological knowledge of seagrass ecosystems compared to other vegetated coastal habitats. Moreover, to date, there are many proxies more widely used in other ecosystems (e.g. lakes, deep marine sediments) that have not yet been used in seagrass paleorecords. For example, macro and microfossils (seagrass macrofossils, dinoflagellates, diatoms, foraminifera), their stable isotopes composition, biogeochemical markers (fossil pigment, lipids), and more specific sediment organic and inorganic composition. This is the case, in particular, of the autochthonous components related to the biological structure and functioning of the seagrass ecosystem. Therefore, it is necessary to continue researching in the paleoecological seagrass field in order to explore the potential information all these proxies can provide.

## 3. STATISTICAL INSIGHTS INTO PALEOECOLOGICAL RECONSTRUCTIONS

A wide range of statistical analyses is applied in the paleoecological field. A brief compendium of the more common and up-to-date techniques used by paleoecologists, as well as the limitations of these techniques, is presented here. Particular emphasis is put on techniques used in this thesis.

### 3.1. The nature of proxies

Proxies are used to reconstruct past environmental conditions qualitatively or quantitatively and to study their reaction to different stressors using numerical methods. The diversity and complexity of proxy data can be exceedingly high, and, these data can be in different units, including relative frequencies, concentrations, accumulation rates, ratios, and the presence or absence data (Birks et al., 2012). Each type of data can provide relevant and different insights, but care should be taken when processing them. Their numerical properties must be considered (e.g., closed percentage data, many zero values, many variables). Some common transformations are standardization to achieve comparability, as well as square roots, logarithms or the Box-Cox transformations, to make data closer to symmetrical distributions. Besides them, some variables may require specific processing before analyses in order to avoid spurious relationships (Birks et al., 2012). For example, closed compositional data require specific numerical methods (Aitchison, 1986; Filzmoser et al., 2018).

### 3.2. The multi-proxy approach and temporal-series analysis

Interpretations based on multi-proxy studies are much sounder and more reliable than those based on a single or very few proxies. Due to the complexity of the interactions in an ecosystem, the more proxies considered, the better and broader will be the overview we get of past environments (Birks & Birks, 2006; Birks et al., 2012). Ordination techniques are widely applied in paleoecology with different intentions: i) to summarize the significant variation gradients by stratigraphically plotting the object scores of each Principal Component Analysis/Correspondence Analysis ordination axes, and to ecologically interpret these gradients using the variable loadings on the ordination axes; ii) to identify and statistically test important explanatory environmental variables (e.g. Redundancy Analysis, Canonical

Correspondence Analysis and their partial relatives, with Monte Carlo permutation tests amongst others, or Generalized Linear Models); iii) to summarize the data in a few groups (zonation) by stratigraphically constrained clustering; and iv) to quantify the relative proportion of variation of a response variable explained by various explanatory variables (variance partitioning) etc... (Birks et al., 2012).

Paleoecological data are considered as temporal-series because they are irregularly spaced in time, and the term 'time-series' is usually reserved for observations made repeatedly at equal time intervals (Birks et al., 2012). The temporal structuring of temporal-series can be quantified to check if they show long-term trends or short-term variations. Cyclical variations or phases of values well above or well below the long-term means or trends can also be determined (Birks, 2012). Temporal trends have been typically assessed either by using simple linear regressions or (non-) parametric correlation coefficients. However, these analyses violate the assumption of independent observations. Running means or Local Estimated Scatterplot Smoothing (LOESS) are techniques also used to estimate trends but with a high inherent subjectivity when choosing its parameters, such as the degree of smoothing. Generalised additive models (GAMs) have been proposed to estimate temporal smooth and non-linear trends but with an automatic and objective selection of the smoothing parameters. They can handle the irregular spacing in time, model temporal autocorrelation if needed and account for model uncertainty (Simpson, 2018).

Another approach in temporal or time series analysis involves the frequency domain, which focuses on bands of frequency or wavelength over which the variance concentrates. It estimates the proportion of the variance attributable to each of a continuous range of frequencies. These spectral analyses can help detect periodicities, which can be attributed to global climatic signals, most of them with cyclical trends. However, most of the spectral analyses require a regular spacing in time as well as stationary data (no trends in mean or variance). An alternative option is to interpolate samples to equal time intervals, but this interpolation is known to underestimate the high-frequency components of the spectrum (Schulz & Stattegger, 1997). It is preferable to use spectral analyses that can handle the original irregular temporal series. For example, the Lomb-Scargle periodogram, successfully applied in paleoecological temporal series together with a permutation test to check the significance of the registered spectral peaks (Lomb, 1976; Scargle, 1983; Pardo-Iguzquiza & Rodríguez-Tovar, 2000, 2011, 2012).

### 3.3. Limitations and perspectives

Records cannot be exhaustively dated due to the cost and time involved, so age distribution along the records has to be modeled based on a limited number of datings. Therefore, paleoecological data has some degree of uncertainty in both the proxies measurements and in their age estimates. These uncertainties are not generally shown in proxy diagrams. It is known, however, that the data are temporally uncertain so it can be "moved" in order to fit to specific hypotheses. If uncertainties are not considered, contextualising the paleoecological data by simply visually comparing them to other records could be branded as lacking enough scientific rigour (Blaauw et al., 2010, 2019).

Despite the limitations mentioned above, the development of statistical techniques at the service of palaeoecology has advanced considerably and is in constant progress (Blaauw et al., 2019). They have a long path yet to tread, especially in the field of quantitative reconstructions. Some of the main problems that have to be faced are those regarding the integration of paleoecological data in models of biological dynamics and data-mining for processing large databases. A relatively new numerical technique used for assessing the effect of predictor variables over a response variable is the additive models (Wood, 2006). These are non-parametric regressions where explanatory variables have additive effects, and the shape between predictor and response variables are determined from the data, rather than pre-assigning a linear or quadratic form. These models can also take into account the temporal nature of the data, being able to model residual temporal autocorrelations (Simpson & Anderson, 2009). Other numerical tools with much potentiality in this field are time-warp analysis, quantile regression, additive modelling, hierarchical partitioning, and Bayesian inference (Birks et al., 2012).

# OBJECTIVES

The overall aim of this PhD thesis is to enlarge the knowledge that paleoecological studies can offer about seagrass meadows, with especial interest in *P. oceanica*, by characterizing the ecosystem dynamics laid in their sediments over the last millennia. Long-term information is essential to identify and understand the ecosystem and its trends, as well as to help to assess plausible future scenarios and their consequences in a changing world.

The general aim can be split into the following specific objectives:

1. **To determine the usefulness of biogeochemical proxies yet unexplored in seagrass sediments (Chapters 1 and 2).**
   The utility of many proxies remained unclear before this thesis work, especially of those related to the autogenic components of the seagrass ecosystem. We have herein attempted (1) to reconstruct the production of the seagrass itself through the use of seagrass macro-debris (sheaths, rhizomes and roots), together with the carbon and nitrogen stable isotope composition of the sheaths, and (2) to reconstruct the paleoproduction of other primary producers inhabiting the meadow, as well as to identify long-term changes in the whole phototrophic community composition by using sedimentary pigments.

2. **To identify the major environmental processes registered in seagrass deposits (Chapter 3).**
   Herein we have used for the first time Fourier-transformed infrared spectroscopy (FTIR) in multiple seagrass deposits with two aims. First, getting a more precise identification of the main organic and inorganic compounds accumulated in seagrass deposits, and second identifying the major biogeochemical processes to which these compounds could be related to. The potential paleoecological interest of these biogeochemical processes is also discussed.

3. **To describe the long-term seagrass ecosystem dynamics and its sources of variability (Chapters 1, 2 and 3).**
   In work available before this PhD research, the dynamics of seagrass ecosystems were mostly characterized at annual to decadal scales. Describing the long-term dynamics of the seagrass ecosystem is, therefore, one of the main objectives of this thesis. Regarding the sources of long-term variability, local and global anthropogenic impacts (current climate change) were claimed to be the primary sources of change in seagrass ecosystems over decadal and even to millennial time scales. However, previous studies have not adequately and statistically addressed the plausible role of natural and larger-scale forcing factors, such as the solar irradiance or regional atmospheric patterns (e.g. López-Merino et al., 2017;

López-Sáez et al., 2009; Mateo et al., 2010; Marbà et al., 2014; Serrano et al., 2011). Here, we aim to identify the main sources responsible for long-term (centennial to millennial) variability of seagrass ecosystem dynamics considering the plausible influence of natural external factors.

4. **To determine the relative influence of local and global forcing factors on the long-term seagrass production (Chapter 4).**

   By using Generalised Additive Models, a quite novel statistical technique, we attempt to estimate the relative influence of local and global factors on the long-term seagrass production along different sites located in the Spanish Mediterranean coast. By doing so, we were able to identify which sites may be more vulnerable to the effects of climate change and in which meadows local management actions could be more effective.

# CHAPTER

# 1

# MILLENNIAL-SCALE TRENDS AND CONTROLS IN POSIDONIA OCEANICA (L. DELILE) ECOSYSTEM PRODUCTIVITY

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# ABSTRACT

*Posidonia oceanica* is a marine phanerogam that buries a significant part of its belowground production forming an organic bioconstruction known as mat. Despite *Posidonia* seagrass mats have proven to be reliable archives of long-term environmental change, palaeoecological studies using seagrass archives are still scarce. Here we reconstruct four millennia of environmental dynamics in the NE coast of Spain by analysing the carbon and nitrogen stable isotopic composition of *P. oceanica* sheaths, the proportion of different seagrass organs throughout the seagrass mat and other sedimentological proxies. The palaeoenvironmental reconstruction informs on long-term ecosystem productivity and nutrient loading, which have been linked to global (e.g., solar radiation) and local (e.g., land-use changes) factors. The long-term environmental records obtained are compared with previous palaeoecological records obtained for the area, showing a common environmental history. First, a relative seagrass ecosystem stability at ~4000 and 2000 cal. yr BP. Then, after a productivity peak at ~1400–800 cal. yr BP, productivity shows an abrupt decline to unprecedented low values. The fluctuations in ecosystem productivity are likely explained by increases in nutrient inputs related to human activities – mostly in the bay watershed – concomitantly with changes in total solar radiation. Cumulative anthropogenic stressors after Roman times may have started to affect ecosystem resilience, dynamics and productivity, with more abrupt regime shifts during the last millennium. These results add into recent research showing the potential of seagrass archives in reconstructing environmental change and seagrass post-disturbance dynamics, hence providing invaluable information for improving the efficiency in managing these key coastal ecosystems.

# 1. INTRODUCTION

Seagrass meadows provide invaluable ecosystem services, as they constitute biodiversity hotspots, improve the quality of coastal waters, stabilize sediments and reduce shoreline erosion. However, they are declining worldwide due to anthropogenic pressures, including global change (Short & Neckles, 1999; Orth et al., 2006a). In recent times, substantial efforts have been invested in preserving seagrass meadows, key in current European environmental policies. Posidonia meadows are protected as a priority habitat (Council Directives, 1992, 1997), as a species (Barcelona Convention, 1976; Bern Convention, 1979), under specific legal protection actions in individual countries (e.g., Albania, Croatia, France, Italy, Spain and Turkey), and included in marine protected areas along the Mediterranean Sea (Pavasovic et al., 2009). Monitoring programs are taken place since the end of the 20th century, such as the Posidonia Monitoring Network in the Provence- Alpes-Côte d'Azur region (PACA) in France, or the POSIMED project along the Mediterranean coast of Spain.

However, monitoring programs present several handicaps, including the limited time-span they cover (i.e., short-term environmental records). Ecosystem dynamics occur at multiple spatiotemporal scales, and the discrimination of centennial and millennial patterns and processes needs an adequate time perspective (Seddon et al., 2014a). Therefore, long-term environmental records are a priority. In this sense, a palaeoecological approach provides long-term environmental records. The longer time span they cover enables the reconstruction of pre-anthropogenic scenarios, the discrimination between natural and human induced perturbations, and the determination of regime shifts as well as the ecosystems' resilience to perturbations (e.g., Willard & Cronin, 2007; Benton & Harper, 2009; Davies & Bunting, 2010; López- Merino et al., 2012). Regime shifts are abrupt changes on several trophic levels leading to fast ecosystem reconfiguration, usually after abrupt climatic changes or anthropogenic impacts (Andersen et al., 2009). Knowing the relevant long-term processes resulting in abrupt ecological changes provides priceless information for guiding ecosystem conservation strategies (Willis et al., 2005, 2007; Davies & Bunting, 2010; Birks, 2012).

*P. oceanica* shows seasonal dynamics in productivity with shoot growth peaking in late summer and declining in fall (Alcoverro et al., 1995, 1997). This annual pattern is mainly regulated by changes in light and water temperature associated with solar insolation (Alcoverro et al., 1995, 1997). Moreover, a feedback control on growth is caused due to seasonal variability in resources and local conditions generated by the seagrass growth. *P. oceanica* growth is controlled by light and temperature in winter, while in summer it is limited by nutrients (Alcoverro et al., 1997). Considering this information, on a centennial to millennial scale it would be expected a productivity pattern regulated by solar irradiance if no other limiting resource or disturbance occurred. Local factors (e.g., nutrients, carbon, redox potential, physical processes) play a major role in growth as limiting factors in meadows with high light availability (Pérez & Romero, 1992; Alcoverro et al., 1995, 1997), especially nutrient availability (Romero et al., 2006). Disturbances may cause deviations from the observed seasonal pattern caused by solar irradiance (Short & Wyllie-Echeverria, 1996). On the one hand, natural disturbances are extreme climatic events, changes in wave exposure and tidal currents, diseases, grazing and bioturbation. On the other hand, human-induced disturbances are eutrophication, dredging, filling and certain fishing practices causing direct physical damage (Short & Wyllie-Echeverria, 1996).

Environmental archives are especially scarce in marine coastal areas owing to high hydrodynamic energy and bioturbation (Mateo et al., 2010). However, *P. oceanica*, a slow-growing and climax seagrass species, amongst the most productive of all marine ecosystems (Duarte, 1991a; Mateo et al., 2006), forms coherent sedimentary sequences with temporal resolution ranging from 2 to 17 yr $cm^{-1}$ (Serrano et al., 2016c).

*P. oceanica* is composed by rhizomes, leaf shoots and roots. The leaves proximal end presents a cylindrical structure known as leaf sheath, attached to the rhizome. The high lignin and phenolic content of the seagrass debris confers them a remarkable decay-resistant nature (Kaal et al., 2016). The annual accumulation of the refractory fraction of the *P. oceanica* organic debris, together with the accumulation of other organic and inorganic particles trapped in the meadow, results in a bioconstruction known as mat (or "matte"; Boudouresque and Meinesz, 1982), consisting in massive pools of organic matter (OM) sequestered over millennia and with a thickness reaching up to 6.5m (Mateo et al., 1997; Lo Iacono et al., 2008; Pergent et al., 2012). The anoxic conditions prevailing in the mat favour the preservation of abiotic and biotic proxies (Mateo et al., 1997, 2006), thus enabling the application of a palaeoecological approach on the *P. oceanica* archive (e.g., López-Sáez et al., 2009; Mateo et al., 2010; Serrano et al., 2011, 2013, 2016b, 2016c; López-Merino et al., 2015, 2017; Kaal et al., 2016).

Soils under *P. oceanica* meadows are usually mixed siliciclastic– carbonate, the carbonate fraction mainly derived from epiphytic carbonate production and the great diversity of calcifying organisms that require the seagrass as shelter, source of food and substrate (Mateu-Vicens et al., 2012; Gaglianone et al., 2017). The main control on the relative abundance of calcareous epiphytes is seagrass biomass. Mature and longer leaves with higher surface area host more epiphytes than the young ones and meadows with higher shoot densities and canopies host more calcifying organisms (Mazarrasa et al., 2015). Moreover, calcification within the meadow is enhanced with the increase of seawater pH due to the photosynthetic activity of the seagrass (e.g. Semesi et al., 2009). Following these premises, the carbonate content in the mat under the meadow could be a proxy of the seagrass productivity. However, if the geological substrate of the bay watershed is dominated by limestone, the carbonate content would not allow the discrimination between the biogenic production and the terrestrial input (Gaglianone et al., 2017).

Despite successful applications of stable isotope ratios in paleoceanography (Koch, 1998; Hayes et al., 1999), their potential to reconstruct changes in seagrass ecosystems remains largely unexplored. The stable isotope composition of plant tissues changes in response to environmental variability (Amundson et al., 2003; Mateo et al., 2004; Cernusak et al., 2013). Positive correlations between stable carbon isotopes ($\delta^{13}C$), solar irradiance and productivity have been reported for *P. oceanica*, opening the possibility of using $\delta^{13}C$ as a proxy for past changes in seagrass productivity, or even in solar irradiance if no other abrupt environmental disturbances occurred (Hemminga & Mateo, 1996; Mateo et al., 2000, 2010).

Nitrogen stable isotopes ($\delta^{15}N$) are more difficult to interpret due to their inherent variability (Fogel & Tuross, 1999). Different processes may influence the N isotope composition in aquatic plants. First, the isotopic signature of available N sources is highly variable (Gaye-Haake et al., 2005). Second, isotopic fractionation during nitrate and ammonium assimilation leads to post-assimilation changes in $\delta^{15}N$ values (Fogel & Cifuentes, 1993; Teranes & Bernasconi, 2000). Finally, bacterial degradation can also lead to a depleted isotopic signal in the residual organic matter during early diagenesis under anoxic conditions (Lehmann et al., 2002). Despite of this variability, $\delta^{15}N$ in aquatic plants has been used to discriminate between external N sources, mainly related to human disturbance (Chappuis et al., 2017).

In this study, we have applied a multi-proxy palaeoecological approach on a four-thousand-year-old *P. oceanica* mat located at the Portligat Bay in NE Spain. We have analysed for the first time biological proxies such as the proportions of sheath-, root- and rhizome-derived debris as well as the C and N elemental and isotopic composition of *P. oceanica* sheaths with the overarching aim of reconstructing the meadow productivity dynamics in order to reveal possible ecological regime shifts and the environmental drivers behind them.

## 2. STUDY AREA

The Portlligat Bay (Cap de Creus Natural Park, NE Spain) is a small and shallow inlet (0.14 km$^2$ and < 10 m deep) connected to the sea by a 213 m opening to the NE. It is a sheltered bay, protected from winds and sea storms. A large part of the bay (41%) is covered by a meadow of *P. oceanica* with an average thickness of ~4.5 m alternating with sandy bioclastic patches (Lo Iacono et al., 2008). The meadow shows a strong phosphorus deficiency (Alcoverro et al., 1995, 1997). There is not a permanent stream providing volumetrically important terrestrial inputs. The latter are instead modulated by run-off and by eventual strong discharges of a torrent, a seasonally active creek flowing into the bay from its NW shore (Fig. 1a).

The climate of the area is Mediterranean xeroteric (Franquesa I Codinach, 1995). The annual precipitation ranges between 200 and 1300 mm and mainly occurs from October to December (average range for 1950–2016, Servei Meteorològic de Catalunya). The bedrock geology of the catchment is mostly composed of phyllites, slates, schists and some quartzites and marbles which date from the Paleozoic (Cartographic Institute of Catalonia, 1997). >50% of the watershed area has very steep slopes (> 60%). Soils are poorly developed, very shallow, fast draining and coarse textured. They have a 0.3% of carbonate and 1.8–4.3% of organic matter contents (Cartographic Institute of Catalonia, 2006).

Mediterranean shrubland dominates the current landscape. It mainly comprises *Cistus monspeliensis* L., *Cistus albidus* L., *Lavandula stoechas* L., *Calicotome spinosa* L., *Ulex parviflorus* Pourr, *Pistacia lentiscus* L., *Juniperus oxycedrus* L., *Arbutus unedo* L., *Quercus coccifera* L. and *Erica arborea* L. Forest cover is sparse, with small areas covered by cork oak trees (*Quercus suber* L.) and pines (*Pinus halepensis* Miller, *Pinus pinea* L.), while *Quercus ilex* L. and *Quercus pubescens* Willd. occur in sheltered areas (Franquesa i Codinach, 1995). The current landscape has been influenced by a long history of human activities, mostly related to farming (Franquesa i Codinach, 1995; López-Sáez et al., 2009, 2015, 2017). However, traditional dry-land farming and fisheries have recently been replaced by tourism, resulting in the abandonment of terraced vineyards (*Vitis vinifera* L.) and pasturelands.

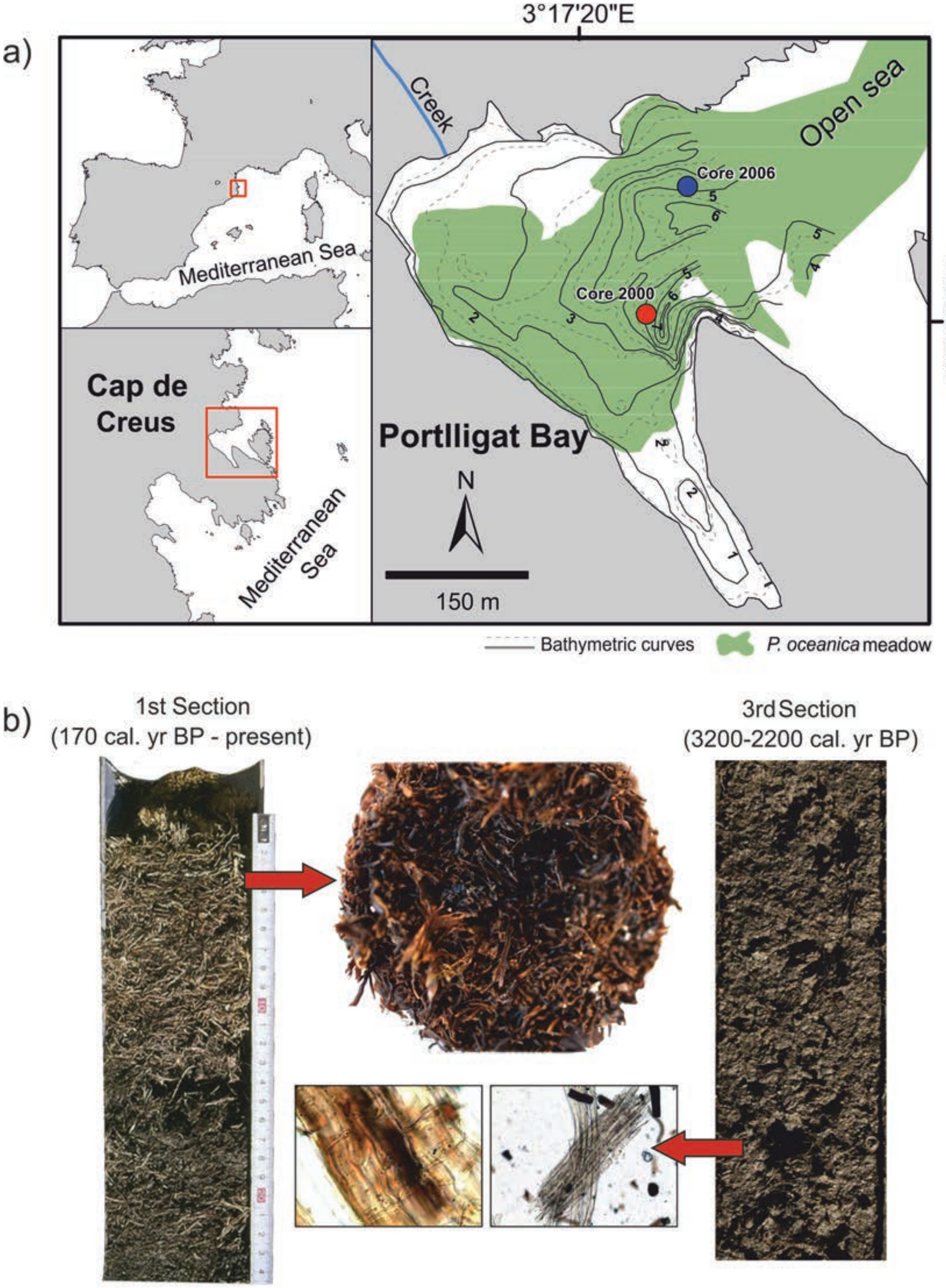


**Figure 1.** (a) Location of the study area and the coring site of Core 2000 (red dot, this study) and Core 2006 (blue dot, López-Merino *et al.,* 2017) (Portlligat Bay, Girona, Spain). (b) Core 2000 shows a dense matte with abundant organic matter for the first forty centimeters, changing to sands (fine to coarse size) with rhizomes, roots and leaf sheaths more degraded in deeper sections.

# 3. MATERIALS AND METHODS

## 3.1. Coring procedures and laboratory analyses

A 475-cm long core of *P. oceanica* mat was obtained in 2000 CE (Core 2000 from now on) from the Portlligat Bay at a depth of ~3 m (42° 17' 32" N; 3° 17' 28" E; Fig. 1a). It was recovered using a floating drilling platform with a self-powered drill, which combined percussion and rotation (see details in Serrano et al., 2012). The stratigraphy showed a dense mat with abundant organic matter for the first forty centimeters, changing to sands (fine to coarse size) with rhizomes, roots and leaf sheaths embedded within the sediment matrix below this depth (Fig. 1b). The core was sliced into 1 cm-thick slices and 176 samples were selected for the analyses. The samples were dried at 70 °C in order to calculate dry bulk density. Soil organic matter <1mm (SOM) was determined by loss-on-ignition (450 °C for 5 h) after dry-sievieng (1 mm) bulk subsamples. Total carbonate content ($CaCO_3$) was measured in bulk subsamples using a Scheibler calcimeter.

Subsamples were wet-sieved in seawater into two fractions, a coarse (> 1 mm) and a fine (1mm ≥ fine > 63 µm) fraction. The coarse fraction was sorted into organic (coarse organic matter, COM, >1 mm) and inorganic fractions. The organic fraction of COM was composed of rhizomes, leaf sheaths and roots, which were separated to account for their biomass. All fractions were dried at 70 °C until constant weight.

Elemental and isotopic C and N composition of *P. oceanica* sheaths were obtained using a Finnigan Delta S isotope ratio mass spectrometer 196 (Conflo II interface). Carbon and nitrogen isotope ratios are expressed as δ values in parts per thousand (‰) relative to the Vienna PeeDee Belemnite and atmospheric $N_2$ (air) standards, respectively. Analytical precision based on the standard deviation of internal standards ranged from 0.11 to 0.06‰.

After wet digestion of the *P. oceanica* sheaths, phosphorus content was measured at the Serveis Científico-Técnics, Barcelona University, using a JobinYvon JI-38 (3600 grooves $mm{-}1$) ICP-AES following Mateo & Sabaté (1993).

Grain size distribution was determined using a Retsch AS 200 analytical sieve shaker for 15 min after wet-sieving (1mm and 0.063mm mesh) with distilled water and removing the COM only. Grain sizes were classified as gravel (> 2 mm), coarse sand (2–0.5 mm), medium sand (0.5–0.25 mm), fine sand (0.25–0.063 mm) and mud (silt and clay <0.063 mm), according to Brown & McLachland (1990).

The carbon and nitrogen stable isotopes, nitrogen and phosphorus content of *P. oceanica* sheaths are original data for this paper, while the other data used were first published in Serrano et al. (2012).

### 3.2. Age depth-model

Serrano et al. (2012) presented an age-depth model for Core 2000 using a smooth-spline model. Here, we used Bacon.R software (Blaauw & Christen, 2011) and the same radiocarbon dates (Table 1). However, while Serrano et al. (2012) discarded two of the fourteen radiocarbon dates, we included them in the model so that the Bacon software could decide whether those radiocarbon dates should be considered outliers. They were finally not discarded. Moreover, we also included the age of the surface of the core, which is the year of recovery (2000 CE). Radiocarbon dates are expressed as calibrated years before present. Dates were calibrated using the marine 13.14C calibration curve (Reimer et al., 2013) and a local marine reservoir correction was applied ($\Delta R=23 \pm 71$ years, Siani et al., 2000).

### 3.1. Numerical exploration

The dataset used for the numerical analyses comprises 176 samples and 16 variables. These variables include: SOM, COM, $CaCO_3$, $\delta^{13}C$, $\delta^{15}N$, carbon, nitrogen and phosphorus contents in sheath remains, sheath debris biomass percentages, root debris biomass percentages, rhizome debris biomass percentages and five sediment grain-size fractions (Fig. 2).

Bulk density, accreation rates, $CaCO_3$, SOM and COM contents were used to estimate mass accumulation rates (MAR) of carbonates and organic matter, following Zachos et al. (2004). MAR are used rather than weight/weight percentages as they better express fluxes (e.g., delivery and preservation). Percentages are influenced by the closed nature of their calculation and, therefore, subjected to dilution/concentration effects (Meyers & Lallier-Vergès, 1999).

After data for each variable were transformed and standardized by subtracting its mean and dividing by its standard deviation, we applied a series of numerical analyses using R software (R Development Core Team, 2011) and CPQtR1.0.3 (Gallagher et al., 2011) in order to detect common trends, main changes, and evaluate the influence of selected factors on the palaeoenvironmental history of the seagrass meadow of the last 4000 years. Compositional data (granulometric distribution, the elemental composition of sheath and organs biomass percentages) were transformed by centered log-ratio (Aitchinson, 1986), while Box-cox transformation method (Box & Cox, 1964) was applied to SOM MAR, COM MAR ($\lambda=0$), and $CaCO_3$ MAR, $\delta^{13}C$, $\delta^{15}N$ in plant debris ($\lambda=1$).

Principal component analysis (PCA) was applied to the variables dataset using the correlation matrix with a varimax rotation, determining the number of significant principal components (PC) with Parallel Analysis (Horn, 1965).

Change-point modelling was applied to all records of PC scores together using a Bayesian transdimensional Markov chain Monte Carlo approach in order to identify common shifts in the trends obtained after the PCA. This approach infers probability distributions for the number and locations in time of changepoints and the mean values between changepoints on several trends (Gallagher et al., 2011).

Using partial redundancy analysis (pRDA), the PC scores were used as 'composite' response variables on which the influence of climate and anthropogenic activity was tested. Five pRDA models were run, one per PC, so one of the PC was the response variable in each of them. All models had the same four explanatory variables. Two explanatory variables were chosen to assess the influence of global climate patterns: Total Solar Irradiance (TSI, Steinhilber et al., 2012) and Northern Hemisphere temperature anomalies (NH temperature, Kobashi et al., 2013). The other two explanatory variables were selected to assess the influence of local factors. They are two records of heavy metals obtained after the PCA of the geochemical composition in sheaths in Core 2000 by Serrano et al. (2011). One record is related to heavy metals derived from anthropogenic activities (PC1m), likely linked to increased soil erosion in the catchment, while the other integrates metals with a more lithogenic and hence, natural geogenic origin (PC2m). All statistically significant pRDA models ($p < .05$) had sample ages partialled out as a covariable.

**Table 1.** Radiocarbon dates in the *P. oceanica* mat sediment Core 2000. The marine13.14C calibration curve was used for calibration and a local marine reservoir effect included (Delta R = 23 ± 71 yr). Radiocarbon dates are taken from Serrano *et al.* (2011).

| Laboratory code | Material type | Depth (cm) | AMS $^{14}$C date (yr BP) | Cal. yr BP (2σ range) | Weighted mean age |
|---|---|---|---|---|---|
| OS-29665 | *P. oceanica* sheaths | 41 | 710 ± 45 | 160 - 400 | 289 |
| OS-29666 | *P. oceanica* sheaths | 62 | 895 ± 45 | 343 - 555 | 461 |
| OS-29667 | *P. oceanica* sheaths | 77 | 975 ± 40 | 468 - 666 | 569 |
| OS-29668 | *P. oceanica* sheaths | 110 | 1430 ± 40 | 697 - 955 | 823 |
| OS-29651 | *P. oceanica* sheaths | 145 | 1600 ± 45 | 913 - 1181 | 1045 |
| OS-44491 | *P. oceanica* sheaths | 213 | 1710 ± 25 | 1269 - 1581 | 1425 |
| OS-44492 | *P. oceanica* sheaths | 255 | 2120 ± 30 | 1572 - 1871 | 1721 |
| OS-44493 | *P. oceanica* sheaths | 287 | 2270 ± 30 | 1821 - 2119 | 1967 |
| OS-44494 | *P. oceanica* sheaths | 307 | 2500 ± 30 | 2005 - 2304 | 2152 |
| OS-44497 | *P. oceanica* sheaths | 326 | 2560 ± 25 | 2184 - 2542 | 2345 |
| OS-44498 | *P. oceanica* sheaths | 355 | 3130 ± 25 | 2570 - 2934 | 2771 |
| OS-44499 | *P. oceanica* sheaths | 386 | 3320 ± 30 | 2947 - 3272 | 3111 |
| OS-44502 | *P. oceanica* sheaths | 415 | 3500 ± 35 | 3236 - 3576 | 3406 |
| OS-44504 | *P. oceanica* sheaths | 437 | 3850 ± 30 | 3473 - 3852 | 3663 |

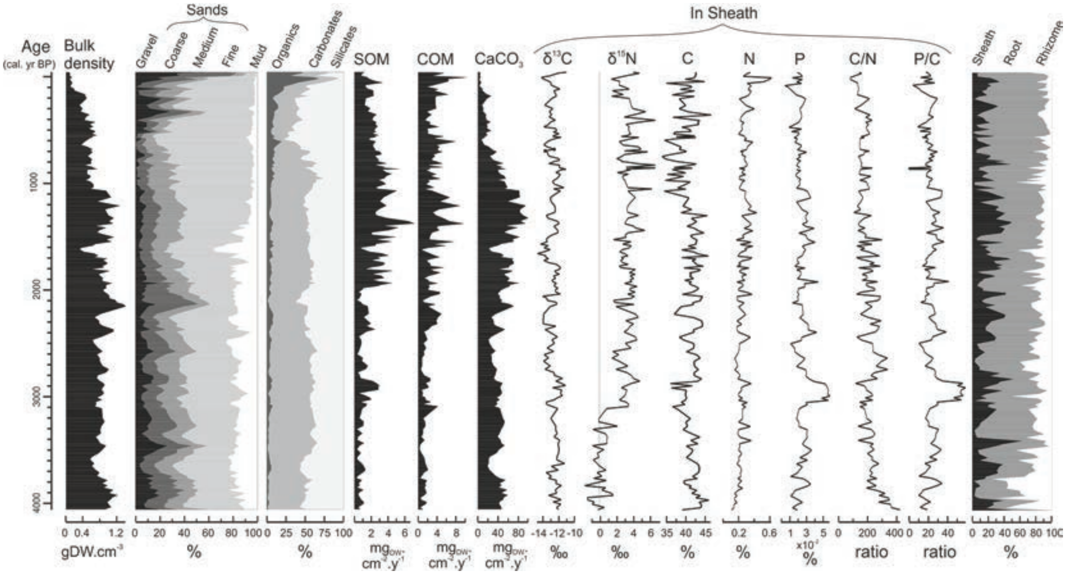


**Figure 2.** Descriptive variables: changes in bulk density, sediment organic matter (SOM), coarse organic matter (COM) and carbonate content, $\delta^{13}C$, $\delta^{15}N$, C, N, P, C/N, C/P, organ debris distribution and grain size distribution along the *P. oceanica* mat sediment Core 2000 plotted against age. The percentage of organics is the sum of SOM (<1 mm) and COM (>1 mm) (i.e., the total organic matter content). Silicates correspond to the percentage of non-carbonate inorganic sediments. Organic matter and carbonate contents are also expressed as MAR (see text for explanation). Stable isotopes and elemental composition were analysed in the sheath debris.

It is important to partial out the statistical effects of age because of the strong temporal autocorrelation, a common feature of time series (Legendre et al., 2002). Most inferential statistical tests assume that residuals are independently and identically distributed, assumption violated if residuals are autocorrelated. Ignoring autocorrelation can result in false inferences. Monte Carlo permutation tests were used to test the significance of the model and of each predictor variable (999 permutations), obtaining the partial explained variation and the significance for every explanatory variable.

Additionally, Lomb-Scargle periodograms – specifically for unevenly sampled times series – were performed to detect statistically relevant periodicities present in the records of PC scores. All data were detrended by linear regression prior to analysis.

## 4. RESULTS

### 4.1. Age-depth model and accretion rates

According to the age-depth model (Fig. 3), the Core 2000 dated back to 4000 cal. yr BP with accretion rates ranging from 0.7 to 1.7 mm $yr^{-1}$ (mean=1.2 ± 0.3 mm $yr^{-1}$) and an average resolution of 8.8 ± 2.4 yr $cm^{-1}$. The 1–295 cm section (~2000–0 cal. yr BP) showed higher accretion rates (mean=1.4 ± 0.2 mm $yr^{-1}$) than the 295–475 cm section (~4000–2000 cal. yr BP) (mean=0.9 ± 0.1 mm $yr^{-1}$, Mann-Whitney U, two-tailed $p < .001$).

### 4.2. Principal component analysis and change point modelling

Five principal components explain 73% of the variance (Fig. 4). The first principal component (PC1) accounts for 24% of the variance, showing positive loadings for SOM MAR, COM MAR, $\delta^{15}N$ and medium and fine sands. The second principal component (PC2) explains 14% of the variance, showing negative loadings for root and rhizome biomass and positive loadings for sheath biomass and nitrogen in sheath. The third principal component (PC3) explains 13% of the variance, showing positive loadings for coarse sands and N in sheath and a negative loading for mud. The fourth principal component (PC4) explains 11% of the variance, showing positive loadings for $CaCO_3$ MAR and $\delta^{13}C$ and a negative loading for root biomass. Finally, the fifth principal component (PC5) explains 11% of the variance, showing a positive loading for P in sheath and a negative loading for C in sheath.

The change-point modelling applied to the five records of PC scores suggests 12 statistically significant regime shifts (change-points CP-1 to CP-12; Fig. 5). Four of them (CP-3, CP-4, CP-7 and CP-8) at the scale of centuries, while the rest are more abrupt, occurring within decades. CP- 6, CP-9, CP-11 and CP-12 are the most abrupt regime shifts.

### 4.1. Influence of explanatory variables

pRDA models for the records of PC scores were all statistically significant (p=.001) except for PC2 (Fig. 6; Table 1 of Supplementary material), and they explained from 15 to 36% of the variance of the response variables.

On the one hand, the variance explained by the pRDA model for PC1 as a composite variable was the lowest (15.3%), PC1m composite variable being the main predictor followed by TSI and its interaction with NH temperature (Fig. 6; Table 1 of Supplementary material). On the other hand, the variance explained for PC3 as a composite variable was the largest (36%). Again, PC1m composite variable explained the largest proportion of variance, followed by TSI. Other second-degree interactions between climatic variables and PC1m composite variable contributed to explain up to 11% of variance. For PC4-composite variable, climatic variables explained 6.5% (comprising TSI, NH temperature and their interaction), quite similar to the 6.9% explained by local factors (PC1m and PC2m composite variables). A contribution of 5.6% by the interactions between local and large-scale factors was also found. The predictor which explained a higher proportion of PC5- composite variable was the interaction between NH temperature and PC2m composite variable (7.1%) followed by the record of PC1m (4.9%).

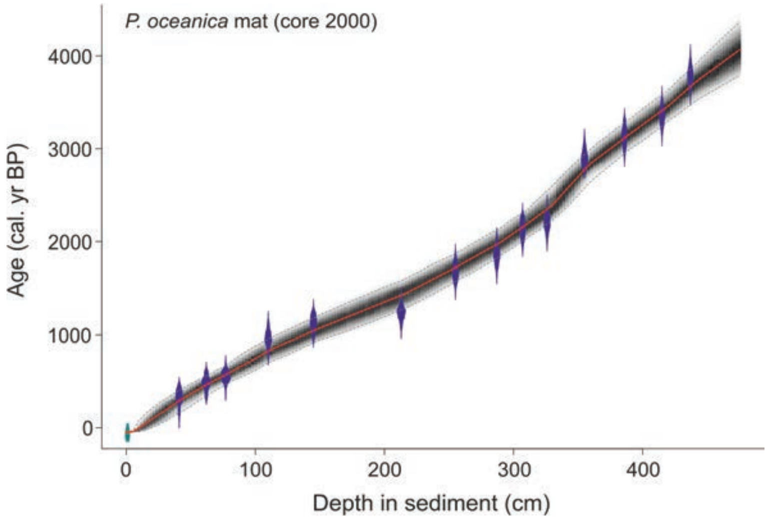
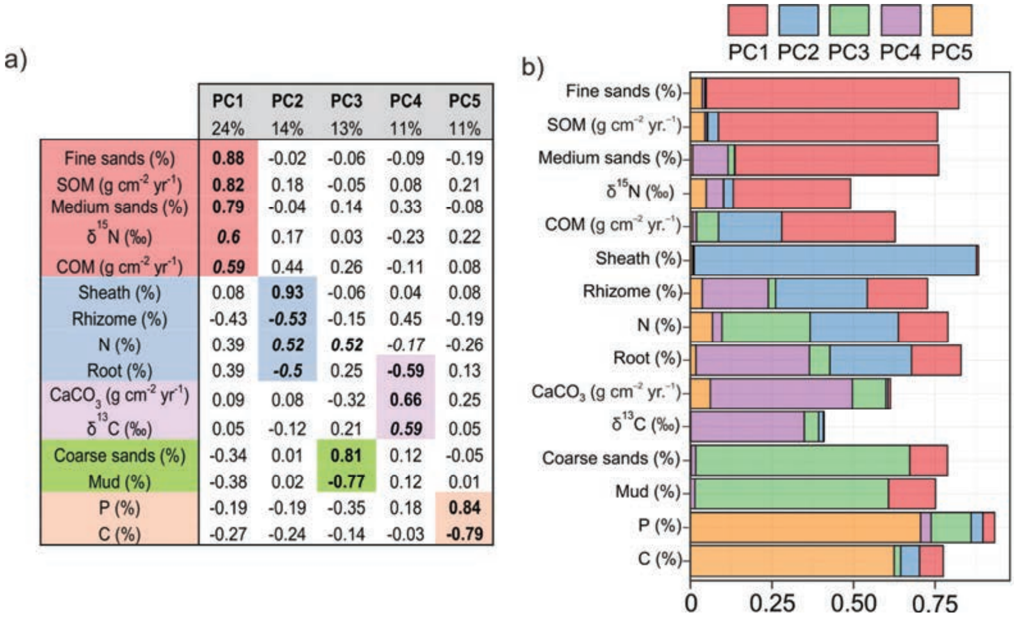


**Figure 3.** Age-depth model of Core 2000 using Bacon.R software (Blaauw & Chrisen, 2011). Fourteen radiocarbon dates were calibrated using the marine13 radiocarbon age calibration curve (Reimer et al., 2013) and corrected for a local marine reservoir effect ($\Delta R = 23 \pm 71$ years, Siani et al., 2000). The red dashed curve shows the "best" model based on the weighted mean age for each depth. Individual radiocarbon dates are shown in probability density functions of calibrated ages. The grey area indicates the uncertainty envelope of the age model with grey dashed curves indicating 95% confidence intervals.


a)

| | PC1<br>24% | PC2<br>14% | PC3<br>13% | PC4<br>11% | PC5<br>11% |
|---|---|---|---|---|---|
| Fine sands (%) | **0.88** | -0.02 | -0.06 | -0.09 | -0.19 |
| SOM (g cm$^{-2}$ yr$^{-1}$) | **0.82** | 0.18 | -0.05 | 0.08 | 0.21 |
| Medium sands (%) | **0.79** | -0.04 | 0.14 | 0.33 | -0.08 |
| $\delta^{15}$N (‰) | ***0.6*** | 0.17 | 0.03 | -0.23 | 0.22 |
| COM (g cm$^{-2}$ yr$^{-1}$) | ***0.59*** | 0.44 | 0.26 | -0.11 | 0.08 |
| Sheath (%) | 0.08 | **0.93** | -0.06 | 0.04 | 0.08 |
| Rhizome (%) | -0.43 | ***-0.53*** | -0.15 | 0.45 | -0.19 |
| N (%) | 0.39 | ***0.52*** | ***0.52*** | *-0.17* | -0.26 |
| Root (%) | 0.39 | ***-0.5*** | 0.25 | **-0.59** | 0.13 |
| CaCO$_3$ (g cm$^{-2}$ yr$^{-1}$) | 0.09 | 0.08 | -0.32 | **0.66** | 0.25 |
| $\delta^{13}$C (‰) | 0.05 | -0.12 | 0.21 | ***0.59*** | 0.05 |
| Coarse sands (%) | -0.34 | 0.01 | **0.81** | 0.12 | -0.05 |
| Mud (%) | -0.38 | 0.02 | **-0.77** | 0.12 | 0.01 |
| P (%) | -0.19 | -0.19 | -0.35 | 0.18 | **0.84** |
| C (%) | -0.27 | -0.24 | -0.14 | -0.03 | **-0.79** |

**Figure 4.** (a) Factor loadings of the descriptive variables of Core 2000 used in the PCA. Numbers in bold indicate variables with factor loadings >0.6 and in bold italics are those with moderate factor loadings (0.5 to 0.6). The individual percentage of variance explained is given under each factor. Factor loadings represent correlation coefficients between the variables and the principal components. (b) Communalities. The communality accounts for the proportion of each variable's variance explained by the five extracted principal components. The total length of the bars is the communality of each element, while the sections represent the proportion of variance allocated in each individual principal component.

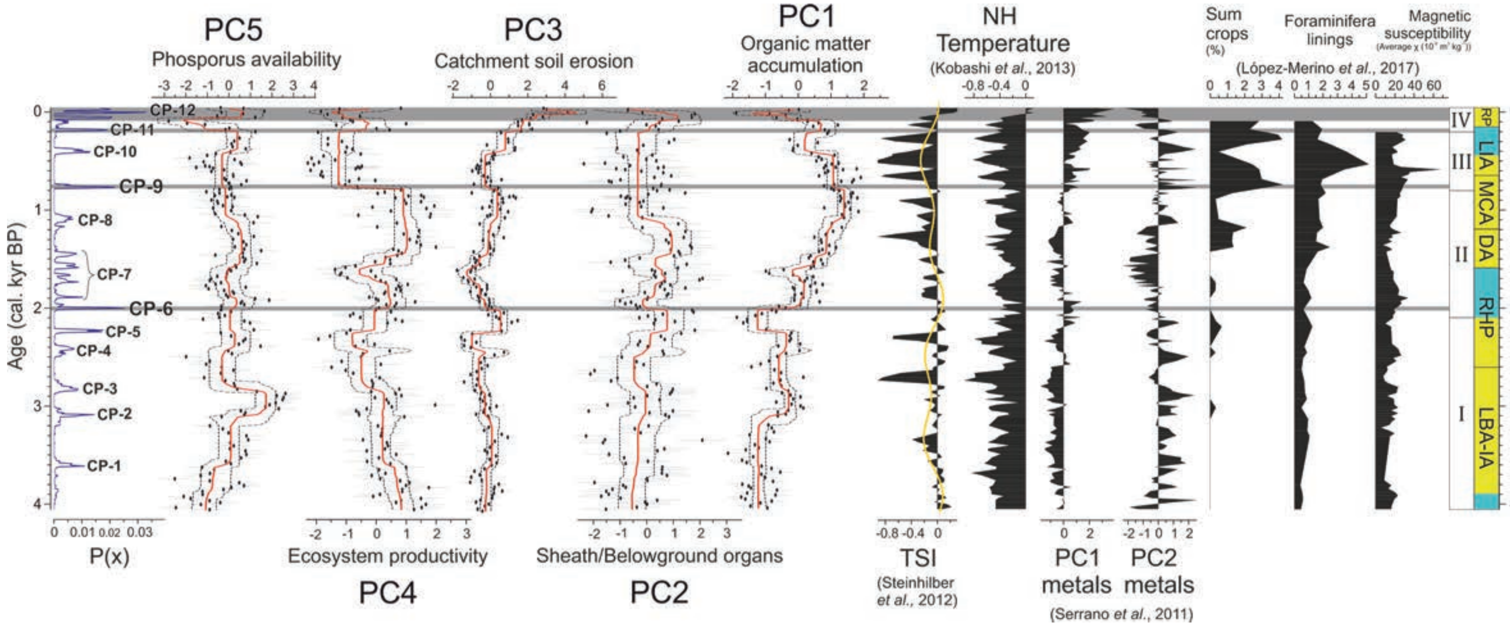


**Figure 5.** Long-term ecological dynamics detected in the *P. oceanica* meadow of Portlligat Bay. Black dots correspond to the original data and horizontal lines are the noise estimation, which is the standard deviation of the unknown error (normal) distribution for a given data set. Thick red curves represent the average after 100,000 functions, while grey lines define 95% confidence interval ranges. The blue curve on the left shows the probability of the change-point [P(x)]. PC: Principal component, CP: Change Point. Horizontal grey bands highlight abrupt regime shifts with high probability.The change point functions are compared to Total Solar Irradiance (TSI), given as difference in $W/m^2$ to the value of the PMOD composite during the solar cycle minimum of the AD 1986 (1365.57 $W/m^2$; Steinhilber *et al.*, 2012); Northern Hemisphere (NH) temperature, given as anomalies (ºC) from AD 1961-1990 (Kobashi *et al.*, 2013); PC1m, considered to be related to anthropogenic activities in the catchment, and PC2m, related to metals with a lithogenic origin (Serrano *et al.*, 2011); sum of crops (Cerealia-t., *Cannabis/Humulus*-t., *Juglans*, *Castanea* and *Vitis*) is a palynological indicator of land-use change; foraminifera linings account for eutrophication of the bay waters and magnetic susceptibility indicates changes in the seagrass mat organic/inorganic content. Sum of crops, foraminifera linings and magnetic susceptiblity data are from Core 2006, a core obtained 150 m apart from Core 2000 (López-Merino *et al.*, 2017). On the right, the four phases identified in this study are indicated as well as arid (yellow) and humid (blue) phases (Pérez-Sanz *et al.*, 2013)

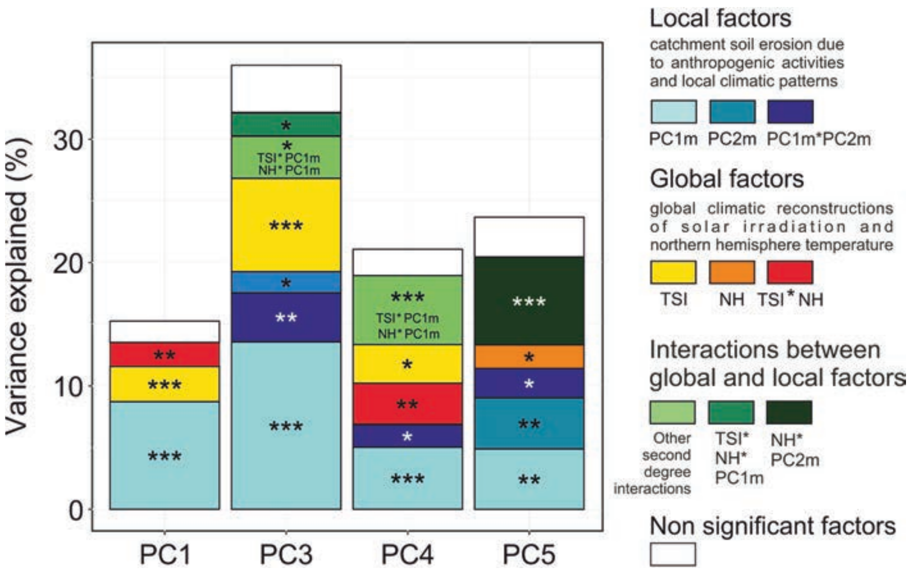


**Figure 6.** Percentage of partial explained variation and significance of individual terms (explanatory variables) assessed using Monte Carlo permutation tests (999 permutations, levels of significance: *p≤0.05, **p≤0.01, ***p≤0.001.) in every partial RDA.

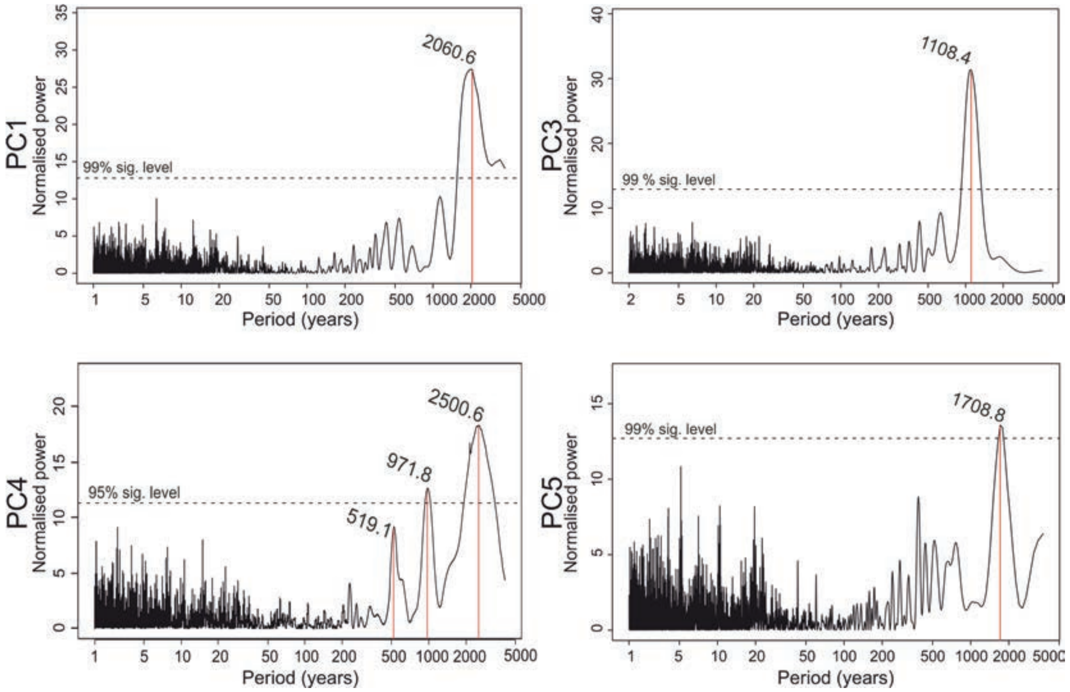


**Figure 7.** Lomb-Scargle normalized periodograms (spectral power as a function of periodicity) of principal components PC1, PC3, PC4 and PC5. The horizontal dotted line marks the significance level. Prominent periodicities are indicated with red lines. There was not any significant cycle observed for PC2.

### 4.1. Spectral analysis

PC3 and PC4 present comparable cycles with periodicities of ~1000 yr (1100 and 970 yr, respectively), while PC1 and PC5 show similar cycles with wavelengths centered at ~2000 yr (2060 and 1710 yr, respectively; Fig. 7). Moreover, PC4 presents a significant periodicity at 2500 yr, as well as one close to significance at 520 yr (Fig. 7). There was not any significant cycle observed for PC2.

## 5. DISCUSSION

### 5.1. Trends in the *P. oceanica* long-term ecosystem dynamics

PC1 seems to indicate changes in organic matter (OM) accumulation and diagenesis (Fig. 4; COM MAR and SOM MAR positive loadings). PC1 positive scores reflect a higher accumulation and lower degree of degradation of OM in the upper section of the mat (Fig. 5; i.e., top ~250 cm, since ~1700 cal. yr BP). The decrease of the score values with depth would be partially related to OM decomposition. $\delta^{15}N$ of sheath debris also shows a positive loading (Fig. 4), most likely linked to a better preserved OM, generally enriched in the heavy isotope (Möbius et al., 2010). In the case of *P. oceanica*, Fourqurean and Schrlau (2003) and unpublished data of project SUMAR (CTM2006–12492/ MAR) reported that $\delta^{15}N$ values decreased substantially during decomposition. The positive loadings that medium and fine sands also show (Fig. 4) are probably related to the fact that the OM <1 mm was not digested prior the granulometric analysis and it may predominate in the fine fractions (< 1 mm), at least in the upper part of the core. Hence, these sands are mostly corresponding to that OM fraction. The changes observed in the OM accumulation indicated by PC1 scores seem to be mainly explained by anthropogenic activities (PC1m) and secondarily by TSI (Fig. 6; Table 1 in Supplementary material). The anthropogenic metal pollution record (PC1m) could be used as an indicator of general human impact, whose main consequence in coastal areas is catchment soil erosion (López-Merino et al., 2017). Changes in catchment soil erosion rates can have a large effect in sediment inputs into the bay and, hence, in the availability of nutrients and oxygen in the seagrass soils, factors known to be key drivers for the decay rates of *P. oceanica* and other aquatic angiosperms remains (Godshalk & Wetzel, 1978a, 1978b; Mateo & Romero, 1996). Climatic variables exert an inherent control on ecosystem productivity (e.g., the effect of irradiance and temperature in photosynthesis), likely affecting the OM supply to the soil.

The positive loading of sheath biomass and negative loadings of root and rhizome (i.e., belowground) biomass in PC2 (Fig. 4) suggest a link with the availability of nutrients in the column water for the plant. PC2 positive scores indicate higher amounts of sheath biomass in comparison with the belowground biomass. The negative relationship between the sheath and the belowground biomass would indicate changes in the allocation of plant biomass, which in seagrasses is related with changes in nutrient concentration change (McGlathery, 2008). The shoot:root ratio increases with high-nutrient availability, while with low-nutrient conditions seagrasses allocate biomass to belowground tissues in order to increase the surface area for nutrient uptake (Powell et al., 1989; Vogt et al., 1993; Pérez et al., 1991, 1994, 2001; Nixon et al., 2001). Furthermore, N in sheath debris also shows a positive loading (Fig. 4), another indicator of higher nutrient availability since N content in tissues increases with higher N availability (e.g., Pérez et al., 2008).

PC3 scores record accounts for the opposite distribution of coarse sands (positive loading) and mud (negative loading) (Fig. 4), likely recording changes in soil erosion. Soil erosion affecting the granulometry of seagrass soils could have different drivers. One driver could be climate, as Mediterranean climate is characterised by sporadic torrential floods resulting in transport of coarser sediments (e.g., Walling et al., 2000; Roca et al., 2009). Land-use change in the catchment could also drive changes in the grain size distribution of the seagrass soils, as it could trigger soil erosion (López-Merino et al., 2017). Coarser fractions in seagrass soils could also be explained by higher local hydrodynamism in the meadow. Higher hydrodynamism (e.g., due to riverflow or runoff waters) causes resuspension and removal of the mud fraction. In fact, PC3 is mostly influenced by anthropogenic activities triggering catchment soil erosion (PC1m) followed by TSI (Figs. 6 and 8; Table 1 in Supplementary material). TSI controls atmospheric and rainfall patterns that also affect catchment soil erosion.

PC4 relates key variables linked to the productivity of the ecosystem. $CaCO_3$ MAR and $\delta^{13}C$ show positive loadings versus the negative loading of root biomass. Carbonates content in seagrasses is consistent with bio-calcification in seagrass meadows and the meadow overall productivity (e.g., Gacia et al., 2003; Semesi et al., 2009). The continental origin of carbonates is less likely than the biogenic source since the phyllosilicate minerals dominate the catchment geology of the Portlligat Bay. The positive loading of $\delta^{13}C$ of sheath would agree with the known positive correlation between $\delta^{13}C$ and seagrass productivity (Hemminga & Mateo, 1996; Mateo et al., 2000). The negative loading of root content fits in the overall picture, as the allocation of biomass to belowground tissue is reduced with high nutrient availability and, hence, productivity (Powell et al., 1989; Pérez et al., 1991, 1994, 2001). PC4 is influenced by anthropogenic activities, as shown by the PC1m record (Fig. 6; Table 1 in Supplementary material). Human impact would be associated with enhanced soil erosion and, therefore, nutrient input. Higher inputs of nutrients and trace metals, such as iron, may stimulate seagrass productivity and sheath biomass production

(Udy & Dennison, 1997; Lee & Dunton, 2000; Marbà et al., 2007). NH temperature and TSI climatic variables also affect PC4 (Fig. 6; Table 1 in Supplementary material), consistent with the positive effect of temperature and irradiance on seagrass productivity (Duarte, 1991b; Pérez & Romero, 1992; Ruiz & Romero, 2001; Nejrup & Pedersen, 2008; Marbà & Duarte, 2009; Mateo et al., 2010; Gacia et al., 2012).

PC5 contrasts P and C contents in sheath, likely linked with the P:C ratio, a known proxy for phosphorus availability in seagrasses (e.g., Duarte, 1990). When the plant is strongly limited by P, its tissues are depleted in this nutrient relative to C content, so the P:C ratio would be lower. As nutrient availability increases, plant tissues become enriched in P relative to the C content, resulting in increasing P:C ratios (Duarte, 1990). PC5 is mainly affected by local factors (PC1m and PC2m), as they influence soil erosion in the watershed which largely controls the delivery of nutrients into the bay (Fig. 6; Table 1 in Supplementary material).

The variance explained by pRDA models ranged from 15.3 to 36%, evidencing that a substantial part of the principal components variability is unexplained by the chosen global and local predictors (Fig. 6; Table 1 in Supplementary material). Other factors that could have played an important role controlling seagrass ecosystem dynamics for the last ~4000 years are local changes in water transparency or temperature – as they can enhance sulphide stress (García et al., 2012) –, dissolved inorganic C availability (Invers et al., 1999, 2001), competition with other primary producers and soil bacteria (e.g., López et al., 1998; Dumay et al., 2002; Alcoverro et al., 2004), or herbivory (e.g., Tomas et al., 2005a).

The spectral analysis showed that soil erosion and productivity (PC3 and PC4) share a periodicity of ~1000 yr; while OM accumulation and P availability (PC1 and PC5) share a periodicity of ~2000 yr. Other periodicities, only linked to productivity (PC4), are 520 and 2500 yr (Fig. 7). Although periodicities may be affected by non-climatic factors (e.g., internal seagrass dynamics), analogous cycles do appear in power spectra of solar activity reconstructions: a ~500 yr cycle, the Eddy cycle (~1000 yr) and the Hallstatt cycle (~2000 yr) (Yin et al., 2007; Dima & Lohmann, 2008; Steinhilber et al., 2012). The 2500 yr cycle could be a fingerprint of the Hallstat cycle, as Yin et al. (2007) observed that its ranges from 2040 to 2400 yr. Therefore, the spectral analysis and the pRDA results provide evidence to support the effect of TSI in the seagrass ecosystem trends.

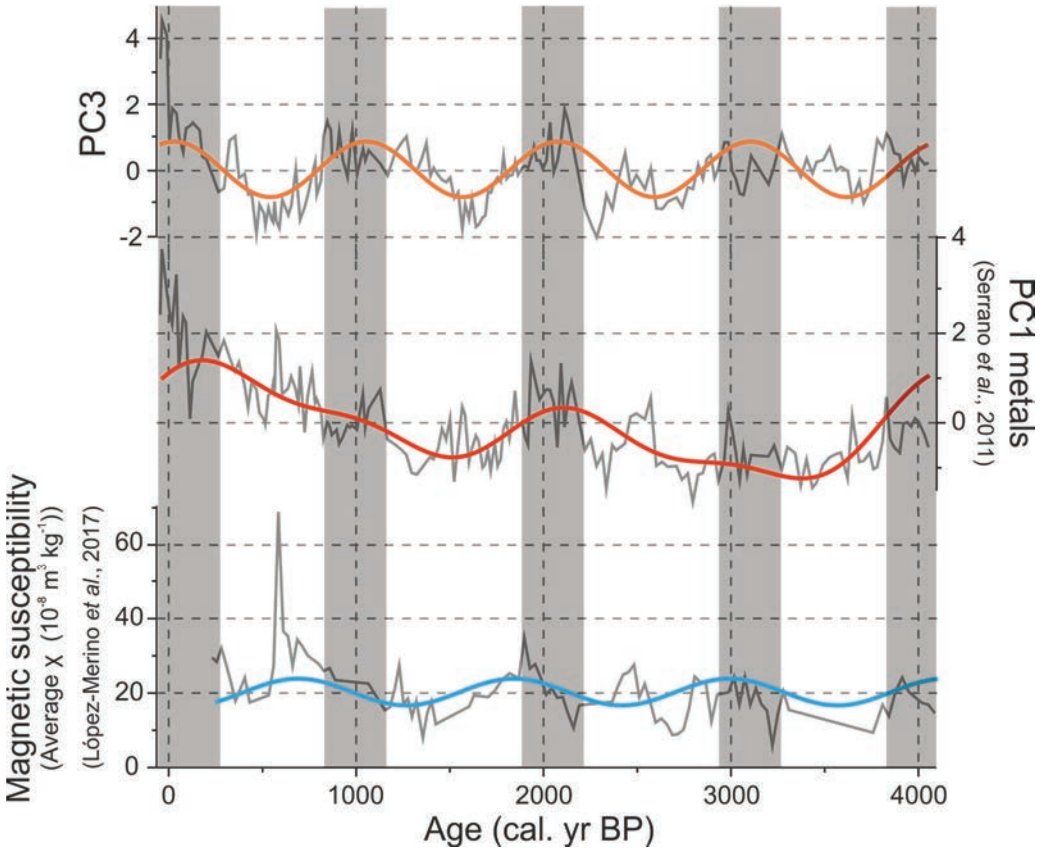


**Figure 8.** Sum of sinusoids fits using periods from Lomb-Scargle periodograms, showing ~1000 years cycles for the soil erosion record (PC3, this study); periods ~4000, ~2000 and ~1000 years cycles for PC1m (Serrano et al., 2011) and period ~1100 for magnetic susceptibility (López-Merino et al., 2017). Vertical grey bands highlight phases of high soil erosion which co-occur with high anthropogenic pressure (PC1m) and high terrestrial inputs (magnetic susceptibility).

The productivity record (PC4) is the only one presenting the three cycles. TSI and productivity trends follow a similar pattern, with intervals of increased TSI associated with increased productivity at ~1000, 2000, 3000 and 4000 cal. yr BP (Fig. 9). Terrestrial ecosystems functioning and photosynthesis depend on downward solar radiation at the Earth's surface (Sinclair et al., 1976; Medvigy et al., 2010). An analogous pattern is followed by *P. oceanica* ecosystems, suggesting that the productivity of underwater vegetation is also sensitive to changes in TSI (Fig. 9). However, even if the detected periodicities are driven by solar cycles, they could also be affected by autogenic mechanisms, subsampling resolution, or a combination of the two factors (Turner et al., 2016).

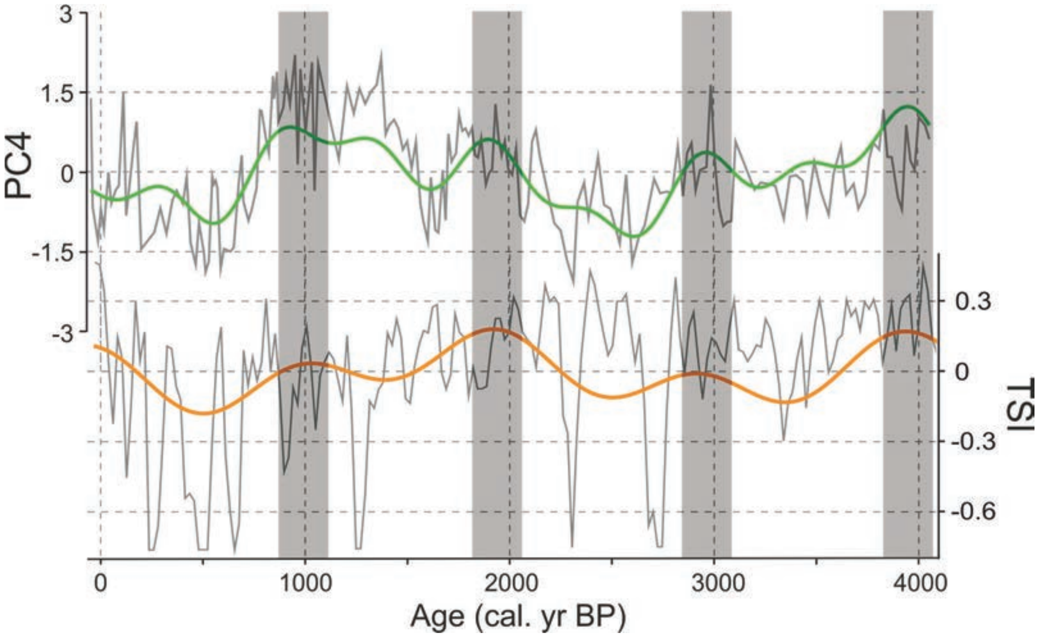


**Figure. 9.** Sum of sinusoids fits using periods from Lomb-Scargle periodograms, showing ~520, ~970 and ~2500 years cycles for the productivity record (PC4) and ~980 and ~2300 years cycles for the Total Solar Irradiance series (Steinhilber et al., 2012). Vertical grey bands highlight phases of solar irradiance maximum, which co-occur with productivity maximum.

### 5.2. Limitations of using $\delta^{13}C$ measured in *P. oceanica* sheath debris as a proxy of productivity

A larger positive loading of $\delta^{13}C$ of plant tissues in the productivity component (PC4) was expected, coherent with the relationships between $\delta^{13}C$ of plant tissues, leaf net production and irradiance found by Mateo et al. (2000, 2010) in field observations and experiments. $\delta^{13}C$ in plant tissues (and derived detritus) responds to changes in the trade-off between C availability and demand, related to light and temperature variations. The long-term ecological results obtained in our work suggest that other factors are superimposed to changes in $\delta^{13}C$ values.

One factor that could affect $\delta^{13}C$ of plant tissues is meadow depth, as the correlation with production and irradiance is weaker in shallow meadows, as in Portlligat, than in those growing closer to the compensation irradiance (Mateo et al., 2000). Assuming no significant changes in sea level for the last four millennia in the area (Vacchi et al., 2016), the depth at which the meadow was growing 4000 years ago would have been around 7 m (3 m water depth at present plus 4 m mat thickness; Lo Iacono et al., 2008). A lower irradiance would have resulted in a lower photosynthetic demand and a higher discrimination against the heavy isotope. Following this rationale, the $\delta^{13}C$ of ancient seagrasses debris should have been more negative than more recent debris. However, no evident trend is found, indicating that this effect is not as important as other factors. Another factor that could affect $\delta^{13}C$ of plant tissues is that the shape of the transfer functions found for the reconstructions was that of a saturation curve (Mateo et al., 2010). This means that resolution of changes in $\delta^{13}C$ at higher productivity levels is lower and consequently changes might not be properly paralleled by the proxy, making the values at the higher end less accurate. Hence, small changes in the $\delta^{13}C$ record would be more meaningful than they seem to be.

The preservation of $\delta^{13}C$ in plant tissues exposed to diagenetic processes is still a long-standing matter of controversy (Wu et al., 2003; Wang et al., 2008; Alewell et al., 2011), questioning its potential as palaeoecological proxy. Microbial reworking of OM during early diagenesis can modify its bulk carbon isotopic content (Meyers & Lallier- Vergès, 1999; Boström et al., 2007). However, there is no clear trend in the literature. According to Meyers and Lallier-Vergès (1999) the overall diagenetic isotope shift in OM isotopic composition in Lake Michigan is minimal, ~1–2‰ shifts towards less negative $\delta^{13}C$ values. Wang et al. (2008) observed differences in $\delta^{13}C$ of up to 2.8‰between vegetation and bottom organic matter. Fourqurean & Schrlau (2003) observed a steady decline in $\delta^{13}C$ of the seagrass *Thalassia testudinum* leaves during decomposition over the course of a year, so that leaves detritus became depleted in $^{13}C$ by ~2‰. This could indicate that variations in underwater soil conditions (e.g., higher nutrient inputs that could increase soil anoxia) could vary the diagenetic effect on $\delta^{13}C$ of the detritus and, hence, blur the correlation between $\delta^{13}C$ in sheaths with TSI and plant production. Preliminary results from in situ degradation experiments of *P. oceanica* sheaths in anoxic conditions (buried at around 10 cm in the sediment), showed no significant changes in $\delta^{13}C$ over 277 days (Project SUMAR, CTM2006-12492/ MAR, unpublished data). Although this is an important finding to support the adequacy of $\delta^{13}C$ for palaeoenvironmental reconstruction, the effect of diagenesis over much longer periods of time remains untested and, therefore, further work is required to validate $\delta^{13}C$ signatures of *P. oceanica* tissues as a proxy of productivity.

## 5.3. Chronology of the environmental and ecological changes

Four phases are distinguished according to the main regimen shifts identified by change point modelling (CP-12, CP-11, CP-9 and CP-6; Fig. 5).

### Phase I: Two millennia of relative stability with a steady decline in productivity (~4000–2000 cal. yr BP)

The records of PC scores showed lower values and variability from ~4000 to 2000 cal. yr BP. The productivity record (PC4) presents high scores at ~4000 cal. yr BP, following a decreasing trend until ~2000 cal. yr BP. The lower scores of the OM accumulation record (PC1) and the record of nutrient availability (PC2) are in accordance with the decreasing trend in ecosystem productivity. This period is described as arid in the Portlligat Bay owing to the abundance of Pinus and evergreen Quercus as well as in other Iberian records by the expansion of Pinus, sclerophyllous and/or steppe taxa (López-Merino et al., 2017 and references therein). The arid conditions occur in the context of a decline in TSI (Fig. 5; Steinhilber et al., 2012).

The first half of Phase I (~4000–3400 cal. yr BP), shows low impact of anthropogenic activities in the area, as indicated by other studies (Fig. 5; Riera-Mora & Esteban-Amat, 1994; López-Merino et al., 2017), suggesting low nutrient supply to the marine environment from soil erosion. The onset of agriculture practices in the catchment is observed by palynological analysis at ~3400–2900 cal. yr BP (López- Merino et al., 2017). Anthropogenic impact steadily increased after ~3400 cal. yr BP, peaking at ~2600–2400 cal. yr BP with an increase in metal pollution due to mining and a larger importance of agriculture (Fig. 5; Serrano et al., 2011; López-Merino et al., 2017).

Overall, Phase I shows a decreasing trend in TSI and an increasing trend in anthropogenic pressure, but still low human impact on the coastal environment. Light seems to have been the main limiting factor for productivity. The strong decline in TSI likely overrided the effect in production derived from higher nutrient availability.

### Phase II: Higher productivity and variability (~2000–800 cal. yr BP)

Throughout this phase, the records of most principal components show higher scores, although with higher variance. Phase II starts with two abrupt changes: CP-5 and CP-6, both taking place during Roman times. An important increase in the coarser sediment fraction, sheath:belowground ratio and productivity are recorded between CP-5 and CP-6. Coarser sediments, along with increased productivity and nutrient inputs, could be explained by the conjunction of more intense human activities (i.e., mining and agriculture) in the catchment during Roman times (Serrano et al., 2011; López-Merino et al., 2017) and to enhanced flooding in eastern Iberia between ~2450 and 2150 cal. yr BP (Benito et al., 2015). Seagrass meadows in Portlligat Bay may have been nutrient-limited; hence anthropogenic- and climate-induced terrigenous inputs would have increased the concentration of nutrients resulting in higher productivity and a lower allocation of resources to belowground tissues.

The record of scores of all principal components reach a minimum at ~1600 cal. yr BP, when crops decreased in the catchment (Fig. 5; López-Merino et al., 2017). Cropping resumed at the onset of the Visigothic period at ~1500 cal. yr BP (Fig. 5; López-Merino et al., 2017). Productivity, sheath:belowground ratio and P availability increased during the Visigothic period, the first two reaching some of the highest values recorded. Therefore, the seagrass productivity at the bay recovered previous levels of production. The end of the Visigothic period is synchronous with another major regime shift, CP-8 (~1400–1050 cal. yr BP). Phosphorus availability and sheath:belowground ratio decrease, while productivity remains constant. The reduction in nutrient supply following the decrease in the agricultural activity at the end of the Visigothic period (López-Sáez et al., 2009; López-Merino et al., 2015, 2017) had no impact on the productivity of the ecosystem. Higher values in TSI could be behind this trend (Fig. 5).

Phase II shows high, constant TSI values, as well as increased nutrient inputs, linked to higher human impact. Despite this, during this phase there is an abrupt change in productivity at ~1600 cal. yr BP coeval with lower evidence of human activities, the overall trend indicates that the seagrass growth over Phase II is regulated by nutrient availability.

### Phase III: abrupt decline in productivity: crossing an ecological threshold? (~800–200 cal. yr BP)

An abrupt change in productivity took place at ~800 cal. yr BP (CP- 9). The region experienced an increase in crops at ~800–600 cal. yr BP, that is reflected in the higher magnetic susceptibility (i.e., soil erosion) of the seagrass mat and in the abundance of foraminifera linings (i.e., eutrophication) as detected in the nearby Core 2006 (Fig. 5; López- Merino et al., 2017). These changes are consistent with rapid deforestation in the area (Riera-Mora & Esteban-Amat, 1994; López-Sáez et al., 2009; López-Merino et al., 2015, 2017). During this chronological interval, TSI exhibits several minima (Figs. 5 and 8), within the context of the Little Ice Age, a climatic anomaly driven by a decline in summer insolation (Mayewski et al., 2004; Steinhilber et al., 2012; Oliva et al., 2018). The combination of low TSI with increasing human impact might have impacted the dynamics of *Posidonia* meadows through diverse and complex mechanisms. First, an excess of sediment and nutrient loadings entering the bay may derive in a poor light environment reinforced by the low TSI, as well as in increased sediment anoxia (Rabalais & Turner, 2001). Second, decreased carbohydrates reserves which are crucial to survive during periods of low TSI (when C balance can be negative) could have compromised the seagrass growth. These decreases in carbohydrates reserves have been observed in the field following nutrient increases since N assimilation requires energy and C skeletons, resources obtained from the carbohydrate reserves (Invers et al., 2004; Alcoverro et al., 2001a). The overall ecosystem resilience seems to have crossed a threshold, causing the sudden regime shift by CP-9 and bringing the system to the lowest levels of photosynthesis and growth.

Between ~600 and 200 cal. yr BP, the coarser fractions and P contents slightly increase, although sheath:belowground ratio, productivity and OM accumulation show low values. This chronological interval is coeval with the establishment of terraced fields of olive trees and vineyards in the area (Franquesa i Codinach, 1995). Terraced agriculture would have limited soil erosion and hence the fluxes of sediments and nutrients into the bay, as attested by the decrease in the abundance of foraminiferal linings (Fig. 5; López-Merino et al., 2017). This lower input of nutrients would explain the lower values of sheath:belowground ratio (Fig. 5).

Although sediment and nutrient inputs into the bay were reduced during phase III, this was not paralleled by a recovery in the productivity levels. The still low prevailing TSI may have kept productivity at its lowest levels, although the crossed threshold in the resilience of the meadow could have meant a change in the functioning of the ecosystem.

### Phase IV: low productivity despite better environmental conditions (~200 cal. yr BP -present)

During the last two centuries, OM accumulation decreases, ecosystem productivity shows low values with no clear trend, the coarser fractions increase, and the sheath:belowground ratio shows higher values. Agriculture practices in the area were progressively abandoned since AD ~1850 due to phylloxera plague damaging the vineyards, and since 1956 CE after a damaging frost (Franquesa i Codinach, 1995). The progressive abandonment of the terraced fields could have enhanced catchment soil erosion, being the reason behind the increase in the coarser fraction, in P content and sheath:belowground ratio.

Briefly, during this phase, even though TSI is higher, the seagrass meadow does not recover its previous state of productivity. This might be because of the trespassed threshold at CP-9.

The results of pRDA for the record of ecosystem productivity composite variable (PC4) show a quite equally distributed variability between local and large-scale factors as well as their interaction (Fig. 6). Therefore, during the last four millennia, the ecosystem productivity has been affected by both human impact and climate, although their importance seems to have varied for the different phases. The long-term perspective of the mechanisms that control productivity in the *P. oceanica* ecosystem provided by the application of a palaeoecological approach on the seagrass mat, is coherent with the controls for the seasonal growth in this species in shallow environments, where local factors can play a major role when light availability is high (Alcoverro et al., 1995).

## 6. CONCLUSIONS

The combination of biological and sedimentological proxies has provided long-term information on the functioning of the *P. oceanica* ecosystem. The multi-proxy analysis has revealed millennial to centennial-scale seagrass ecosystem dynamics through changes in the OM accumulation in the mat, ecosystem productivity, nutrient supply and catchment soil erosion. Global (TSI and NH temperature) and local (anthropogenically-derived nutrient and sediment inputs) factors, as well as their interactions, have played a role in the dynamics of the *P. oceanica* ecosystem throughout the last four millennia.

Although the multi-proxy approach has provided invaluable long-term information on ecosystem changes, the knowledge gaps on the relationships between the proxies used and the environmental factors they are supposed to represent should not be ignored. More integrated studies are needed in order to get a better understanding of catchment-bay interactions, since local factors in the catchment seem to be as important as the climate effects.

The results obtained here, together with the overall ecosystem trends identified, largely match with those found by López-Merino et al. (2017) for another core at the same study area (150 m apart) and using another set of proxies. This reinforces our confidence in the robustness of the approach and the usefulness of palaeoecology as a tool for conservation. An overarching recommendation to be drawn from this study is the need of extending the observation level at the catchment scale if we do not want to overlook key factors that can bring coastal ecosystems close to crossing critical thresholds beyond their resilience.

## APPENDIX[1]

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[1] See supplementary materials in Appendix A.

# CHAPTER

# 2

# FACTORS REGULATING PRIMARY PRODUCERS' ASSEMBLAGES IN POSIDONIA OCEANICA (L.) DELILE ECOSYSTEMS OVER THE PAST 1800 YEARS

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# ABSTRACT

Posidonia oceanica (L.) Delile meadows are highly productive coastal marine ecosystems that provide multiple ecosystem services. The seagrass is not always the major contributor to total primary production, however, little is known about long-term changes in the composition of primary producers within seagrass meadows. Understanding compositional shifts within the community of primary producers is crucial to evaluate how climate and anthropogenic change affect the functioning of seagrass ecosystems. Here we analysed marker pigment composition in seagrass cores from two bays of the Cabrera Island (Balearic Islands, Spain) to assess long-term changes in phototrophic community composition and production in seagrass meadows, and identify the environmental factors triggering those changes. The proxy dataset was explored using principal component analyses (PCA): one including the pigment dataset to look for associations between producers' groups, and another one combining the pigment dataset with plausible local and global regulatory factors to assess the environmental drivers of change. Analyses of characteristic pigments and morphological fossils (cysts) showed that the abundance of dinoflagellates increased over the last 150–300 years, coeval with a rise in solar irradiance and air temperature. When compared among embayments, pigments from cyanobacteria predominated in seagrass meadows located at Es Port, a sheltered bay receiving higher terrestrial runoff; whereas pigments from diatoms, seagrasses and rodophytes were more common at Santa Maria, an exposed bay with clearer waters. Water depth also played a role in controlling the phototrophic community composition, with greater abundance of diatoms in the shallowest waters (<5 m). Overall, our results suggested that historical and spatial variation in seagrass meadows' phototrophic community composition was influenced by the interaction between local factors (catchment-bay characteristics) and global climate processes (energy influx). Together these patterns forecast how marine primary producers and seagrass ecosystem structure may respond to future global warming.

# 1. INTRODUCTION

*Posidonia oceanica* seagrass meadows are one of the most valuable habitats in the Mediterranean Sea owing to their multiple ecosystem services (Spalding et al., 2003). However, this endemic species has exhibited widespread decline since the early 20th century, mainly due to local anthropogenic pressures such as coastal development, pollution, trawling, fish farming, moorings, dredging, dumping and introduced species (Boudouresque et al., 2009b). Fortunately, de los Santos et al. (2019) showed that seagrass loss rates recently slowed down due to effective conservation and restoration actions, including habitat protection. Despite this promising news, relatively little is known about how *P. oceanica* meadows have varied historically in response to perturbations.

Therefore, elucidation of the long-term dynamics and environmental drivers of ecosystem change is required to evaluate the magnitude of current declines in a historical context, as well as to predict, prevent or mitigate the effects of present and future environmental changes on seagrass meadows structure and function (López-Merino et al., 2017; Leiva-Dueñas et al., 2018).

Total primary production of seagrass ecosystems does not always depend on the seagrass species as the major contributor. Other primary producers inhabiting the meadows can contribute substantially (up to 60% of total production), including epiphytes, phytoplankton, phytobenthos and macroalgae (McRoy & McMillan, 1977; Borowitzka et al., 2006; Mateo et al., 2006). The abundance and composition of primary producers' communities within seagrass meadows are regulated by complex mechanisms reflecting interactions between physico-chemical (e.g., light, temperature, water movement, nutrients) and biological factors (e.g., competition for space, grazing and predation) (Koch, 2001; Borowitzka et al., 2006) (Fig. 1). Regulation of composition at the decadal-scale appears to mainly involve competition for light and nutrients between micro- and macroalgae and the seagrass (Delgado et al., 1999; Hemminga & Duarte, 2000; Ralph et al., 2006). Elevated nutrient concentrations favour phytoplankton blooms, as well as epiphyte and macroalgae overgrowth, all leading to attenuation of irradiance and diminished transmission to the seagrass canopy (McGlathery et al., 2007; Viaroli et al., 2008) (Fig. 1).

Epiphyte composition in seagrass leaves is influenced by complex interactions between nutrients, light, temperature, water motion, salinity, and seagrass physiological and phenological characteristics, as well as the biotic interactions between epiphytes, herbivores and predators (Armitage et al., 2006; Lavery et al., 2007; Prado et al., 2007a; Mabrouk et al., 2014a).

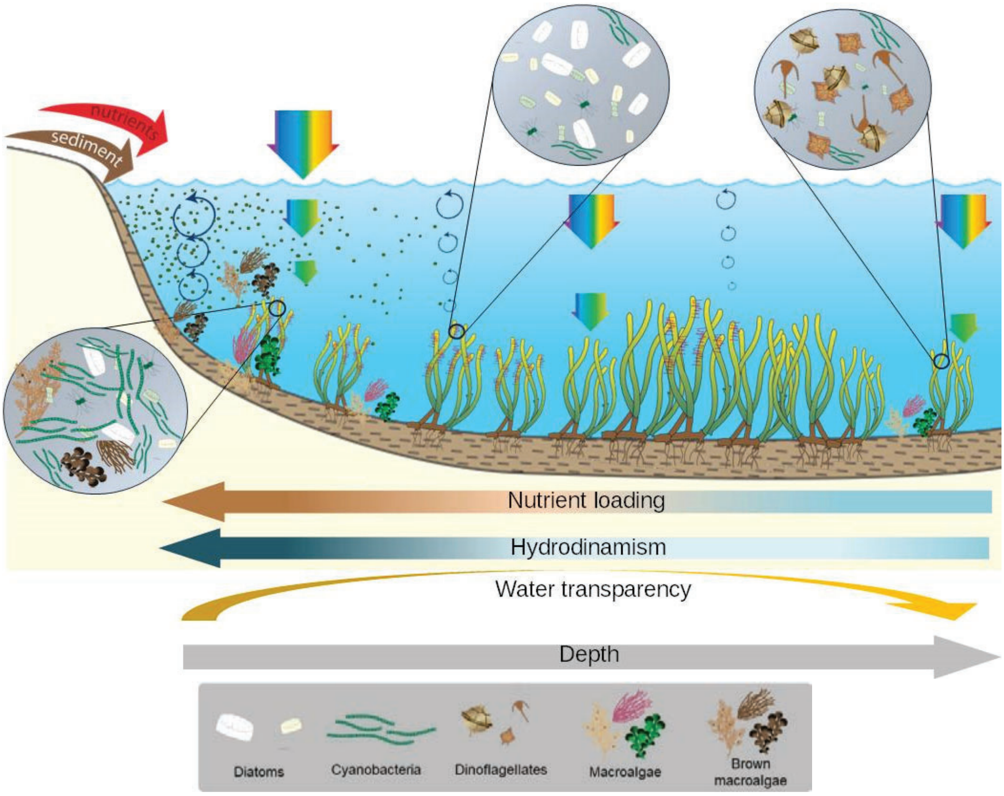

**Figure 1.** Schematic diagram illustrating how nutrient and sediment inputs affect aquatic primary producers in seagrass meadows. Zooms are for micro-epiphytic community composition. Diagram made using image vectors from Image library in Integration and Application Network (ian.umces.edu).

In addition, epiphyte assemblages often vary predictably along a depth gradient due to changes in light, local hydrodynamics, and meadow structure (Borowitzka et al., 2006; Tsirika et al., 2007; Nesti et al., 2009; Piazzi et al., 2016) (Fig. 1).

Research on the factors regulating the complex interactions influencing coastal marine ecosystem production and composition over centennial timescales lags behind that of lacustrine and terrestrial habitats, mainly because of the relative scarcity of reliable coastal marine archives owing to their hydrodynamism (Hay, 1974; Mateo et al., 2010). *P. oceanica* meadows are an exception, since coherent sequences with high temporal resolution (2-17 yr $cm^{-1}$) can be obtained in them (Serrano et al., 2012, 2016a). These *Posidonia* environmental archives, known as mats, consist of large pools of organic matter accumulated over millennia, mainly as decay-resistant plant debris and organic or inorganic remains of other meadow-inhabiting organisms (Mateo et al., 1997; Lo Iacono et al., 2008; Kaal et al., 2016). Therefore, mats can potentially preserve a wide range of biotic and abiotic proxies due to the prevailing anoxic conditions (Mateo et al., 2006; Piñeiro-Juncal et al., 2018).

Proxy analyses on *Posidonia* mats allow quantification of diverse long-term environmental and ecological changes as, for example, the impact of land-use change and metal pollution on coastal systems, the role of climatic factors and seagrass revegetation in carbon burial, and historical variation in seagrass productivity (López-Sáez et al., 2009; Mateo et al., 2010; Serrano et al., 2011, 2013, 2016b, 2016c; Macreadie et al., 2015; Marbà et al., 2015; López-Merino et al., 2015, 2017; Leiva-Dueñas et al., 2018). To date, however, fossils pigments from phototrophic organisms have not been used to quantify long-term changes in the production or gross community composition of seagrass systems, unlike studies on some other marine systems (Kowalewska et al., 2004; Rabalais et al., 2004; Reuss et al., 2005, 2010).

Aiming at filling the abovementioned knowledge gap, we measured past changes in concentrations of fossil pigments from diverse phototrophic organisms, in combination with other proxies (e.g., sedimentological, geochemical and dinoflagellate cysts), in five *P. oceanica* mat cores from two bays of the Cabrera National Park, Balearic Islands, Spain. The objectives of this study were: (1) to measure the variability in pigment composition through time and across spatial gradients (water depth within a bay) in two bays with contrasting features, and; (2) to identify the long-term environmental drivers which may regulate the phototrophic community composition in the meadows.

# 2. MATERIAL AND METHODS

## 2.1. Environmental setting and coring procedures

The Cabrera Island is the largest island of the Cabrera Archipelago, located south of Mallorca (Balearic Islands) in the western Mediterranean Sea (Fig. 2). The climate of the island is semi-arid and although the precipitation is scarce, several small watersheds are active only during intense precipitation periods (Alcover et al., 1993). The main watershed drains into Es Port Bay (Rodríguez-Perea & Servera, 1993). The surrounding coastal waters are warm with very low nutrient content comparing to other coastal Mediterranean waters (Ballesteros & Zabala, 1993).

Five *P. oceanica* mat cores were taken in June 2015 from meadows growing in two bays: Santa Maria (SM), and Es Port (EP) (Fig. 2). Cores were collected at a single station 5-m below the sea level (bsl) at EP and along a depth-transect (5, 10, 15, and 25 m bsl) at SM (Table 1). SM is a relatively exposed bay with an area of 1.14 km$^2$ (55 m maximum depth) connected to the open sea by a 1.2-km wide mouth. On the contrary, EP (0.8 km$^2$, 45 m maximum depth) forms a relatively sheltered environment with a narrower opening (650 m) (Fig. 2). Cores were collected by scuba divers using high-density PVC pipes fitted with core catchers and a serrated leading edge. Exponential decompression functions were applied to correct for core shortening (Morton & White, 1997; Serrano et al., 2012).

At both bays, *P. oceanica* grows on biogenic, carbonate-rich and iron-deficient sediments (Holmer et al., 2005; Marbà et al., 2008). About 42% of SM benthos is covered by dense, continuous *P. oceanica* meadows, whereas meadows in EP cover less area (36%) and occur at a shallower depth (Marbà et al., 2002). Demographic analysis indicates that while meadows at SM are in good condition, those at EP exhibit symptoms of stress, including lower leaf production rates and vertical rhizome elongation, very low shoot recruitment, higher mortality, and elevated sulphate reduction rates. The different seagrass conditions between bays have been attributed to contrasting water residence times in EP (7-15 days) and SM (4 days) (Marbà et al., 2002; Orfila et al., 1992, 2005), and to more frequent and intensive anthropogenic activities at EP (Marbà et al., 2002).

## 2.2. Sedimentology, geochemical analyses and core chronology

Cores were cut longitudinally and opened into two halves. One-half was analysed non-destructively for elemental composition using X-ray fluorescence (XRF) with an AVAATECH core scanner at the CORELAB laboratory, University of Barcelona. One cm-thick samples from one of the half-cores were dried at 60 ºC until constant weight to determine dry bulk density, then homogenized using an automated agate mortar (Mortar Grinder RM-200 RETSCH).

Organic matter content (OM) was estimated in the samples by mass-loss-on-ignition at 550º for 4h. Sediment grain size was determined using a laser-diffraction particle analyser (Mastersizer 2000, Malvern instruments Ltd., UK). Carbon and N elemental and isotopic composition of sediment samples were analysed at UH Hilo Analytical Laboratory, University of Hawaii at Hilo, on a Thermo-Finnegan Delta V IRMS isotope ratio mass spectrometer coupled with a Costech elemental analyser.

Isoprenoid glycerol dialkyl glycerol tetraether (GDGT) lipids were used to calculate the Branched and Isoprenoid Tetraether (BIT) index, an index of the relative abundance of terrestrial and autochthonous organic matter in marine sediments (Hopmans et al., 2004). The samples polar fraction were analysed for GDGTs according to Schouten et al. (2007). GDGT analyses were performed using liquid chromatography–mass spectrometry (LC–MS) with a Hewlett Packard1100 Series instrument equipped with an auto-injector and ChemStation chromatography manager software.

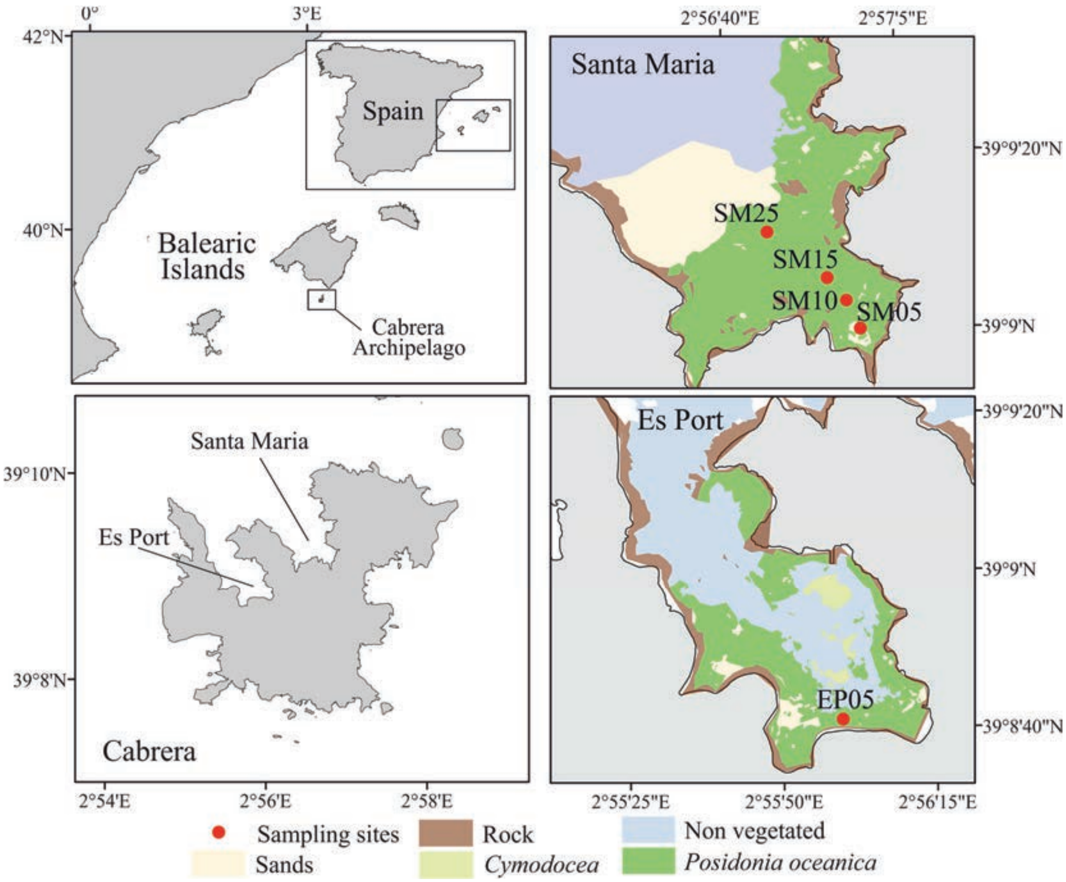

**Figure 2**. Location of the Cabrera Archipelago as well as P. oceanica and Cymodocea meadows areal coverage in two bays: Santa Maria (SM) and Es Port (EP). Red dots indicate the core locations. The number stands for the sampling water depth (in meters below sea level).

**Table 1.** Details of the five cores taken from *Posidonia oceanica* meadows at two bays in the Cabrera Island (Balearic Islands, Spain).

| **Core ID** | **Coordinates** | | **Sampling location** | **Water depth** (m) | **Comp. length** (cm) | **Decomp. length** (cm) | **Compression** (%) |
|---|---|---|---|---|---|---|---|
| **SM05** | 39°9'0"N | 2°56'57"E | Santa María Bay | 5 | 49 | 83 | 42.4 |
| **SM10** | 39°9'3"N | 2°56'55"E | Santa María Bay | 10 | 134 | 161 | 18.3 |
| **SM15** | 39°9'6"N | 2°56'53"E | Santa María Bay | 15 | 113 | 138 | 19.3 |
| **SM25** | 39°9'12"N | 2°56'44"E | Santa María Bay | 25 | 84 | 89 | 5.6 |
| **EP05** | 39°8'42"N | 2°55'60"E | Es Port Bay | ~ 5 | 88 | 98 | 17 |

"Comp." and "decomp." stand for compressed and decompressed.

Radiocarbon ($^{14}C$) and lead-210 ($^{210}Pb$) activities were measured using accelerator mass spectrometry (DirectAMS laboratory) and alpha spectrometry (Environmental Radioactivity Laboratory, Autonomous University of Barcelona), respectively, to obtain age-depth models for the collected cores.

Raw proxy data trends are presented in Fig. S1.

## 2.3. Fossil pigment analysis

Pigments and their derivatives were extracted, isolated, identified and quantified using high-performance liquid chromatography (HPLC) with an Agilent model 1100 instrument at University of Regina following standard methods of Leavitt & Hodgson (2001). Fossil pigment interpretations were restricted to a subset of carotenoid and chlorophyll biomarkers that commonly preserve in sedimentary deposits (Table 2). Predominant phorbins identified included metrics of total primary producers such as labile Chlorophyll-*a* (chl-*a*; a precursor), pheophytin *a* (Chl's stable product), and chlorophyte markers (chl-*b*, pheophytin *b*). Pigment preservation index (PPI) was calculated from the ratio of chl-*a* to its degradation product pheophytin *a*. Complete fossil pigment profiles are presented in Fig. S2.

**Table 2.** Pigments identified in the *P. oceanica* mat cores in this study as well as their taxonomic affinities.

| Pigment | Algal group(s) |
|---|---|
| Alloxanthin | Cryptophytes |
| Diadinoxanthin | Dinoflagellates, diatoms, chrysophytes |
| Diatoxanthin | Diatoms, chrysophytes |
| Lutein- Zeaxanthin | Higher plants, chlorophytes, rhodophytes*, cyanobacteria |
| Echinenone | Total cyanobacteria |
| Canthaxanthin | Nostocales cyanobacteria |
| β-carotene | Total phototrophs |

*In marine ecosystems, lutein-zeaxanthin also represents the Rhodophyta (Esteban et al., 2009).

## 2.4. Organic-walled dinoflagellate cysts analysis

A palynological analysis of pollen and non-pollen palynomorphs (NPP) of the cores is currently under way. Among the NPP, we have identified organic-walled dinoflagellate cysts (dinocysts); microremains relevant for this study due to their relationship with some of the analysed pigments. The results from core EP05 and the preliminary results from core SM25 are presented herein. Pollen and NPP were isolated from seagrass deposits using standard palynological extraction protocols, including sediment digestion with HCl, NaOH and HF to eliminate carbonates, humic acids and silicates, respectively (Fægri & Iversen, 1989). Dinocysts were identified and counted using light microscopy at ×400 magnifications.

## 2.5. Numerical procedures

Principal component analysis (PCA) was used to explore potential associations in the community of primary producers as recorded by fossil pigment concentrations in the cores ($PCA_{pigments}$). Fossil pigment data were reported in units of concentration and, as such, are compositional data which required isometric log-ratio transformation prior the analysis (Aitchison, 1986; Egozcue et al., 2003; Filzmoser et al., 2010). The analysis consisted in a robust PCA via *pcaCoDa* command in "*robcompositions*" package in the R computational environment (Templ et al., 2011).

To determine which environmental variables were the most influential on pigment marker composition, another robust PCA was run including both local factors and global climate indicators ($PCA_{environmental}$). Local factors included biotic variables such as total primary production (as chl-*a*, β-carotene and OM), nutrient cycling and organic matter supply (C and N stable isotope values and BIT index), as well as abiotic descriptors (sediment grain size, and C and N elemental composition, XRF-measured elements). Global climate external factors included indices of Total Solar Irradiance (TSI, Vieira et al., 2011), Northern Hemisphere Temperature (NHT, Kobashi et al., 2013) and the North Atlantic Oscillation (NAO; Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012) - NAO is an atmospheric mode affecting the hydrological variability in the western Mediterranean (Roberts et al., 2012).

Generalized additive models (GAMs) were used to estimate temporal trends in the principal components scores and dinocyst concentrations. GAMs are able to model non-linear relationships between time and a response variable and can handle the irregular spacing typical in palaeoecological time series (Simpson, 2018). Thin-plate regression splines were used to parametrise the smooth functions of time (Wood, 2003). The differences between the fitted smooth functions for $PC1_{pigments}$ scores and concentrations of dinocysts were calculated as in Rose et al. (2012). GAMs were performed using the mgcv package in R (Wood, 2004, 2016, 2017).

*All statistical* analyses were conducted using R statistical software (R Core Team, 2018) and detailed descriptions of the materials and methods section are given in Supplementary Material.

# 3. RESULTS

## 3.1. Age-depth models

The age-depth models combining radiocarbon and $^{210}$Pb dates revealed that core SM15 extended back to ~1900 cal. yr BP, whereas cores SM25 and EP05 extended to ~1700 cal. yr BP (Table 2, Fig. 3A). Cores SM05 and SM10 encompassed less time, SM05 dated back to ~100 and SM10 to ~700 cal. yr BP. Overall, accumulation rates varied between 0.02 and 2 cm/yr with significant differences among cores (median Kruskal-Wallis test, $p<0.05$). A nonparametric pairwise multiple comparison (Dunn's test, $p<0.05$) confirmed all median rates were significantly different except for the pair EP05 - SM15 ($p=0.754$). Accumulation rates decreased with increasing water depth in SM, from a median of 0.36 cm/yr (SM05) to a median of 0.06 cm/yr (SM25) (Fig. 3B). In most cores, mat accumulation was likely continuous with the exception of EP05 which exhibited an apparent hiatus between ~ 300 and ~1250 cal. yr BP - based on a large jump of ~950 calibrated years between two radiocarbon dates at 60 and 64 cm depth in the core (Fig. 3A and Table 3).

## 3.1. Primary producers' composition

Trends in the pigment composition within all cores were well described using a robust PCA with two principal axes, explaining 91% of the total variance (Fig. 4A). The first principal component ($PC1_{pigments}$, 78%) showed a high positive loading for diadinoxanthin (dinoflagellates, diatoms and chrysophytes) and moderate negative loadings for echinenone (total cyanobacteria), lutein-zeaxanthin (chlorophytes, higher plants, rhodophytes and cyanobacteria) and canthaxanthin (Nostocales –cyanobacteria–) (Fig. 4A and Table 4). The second principal component ($PC2_{pigments}$, 13%) showed high positive loadings for diatoxanthin (mainly diatoms) and lutein-zeaxanthin (chlorophytes, higher plants, cyanobacteria and rhodophytes), and high-to-moderate negative loadings for echinenone (total cyanobacteria) and canthaxanthin (Nostocales –cyanobacteria–) (Fig. 4A and Table 5).

The main temporal trend observed in all cores was an increase in $PC1_{pigments}$ scores towards the present, particularly during the last ~150-300 years. This trend mainly reflects increasing concentrations of diadinoxanthin (Fig. 4B).

Sample scores from $PC2_{pigments}$ did not show a consistent change through time, although they did show an evident spatial pattern, with different pigment composition between bays (Fig. 4). Higher proportions of diatoxanthin and lutein-zeaxanthin were found in SM, while canthaxanthin and echinenone predominated in EP. Within SM, sample scores indicated a greater abundance of diatoxanthin and lutein-zeaxanthin in the shallowest area (SM05) of the bay (Fig. 4B).

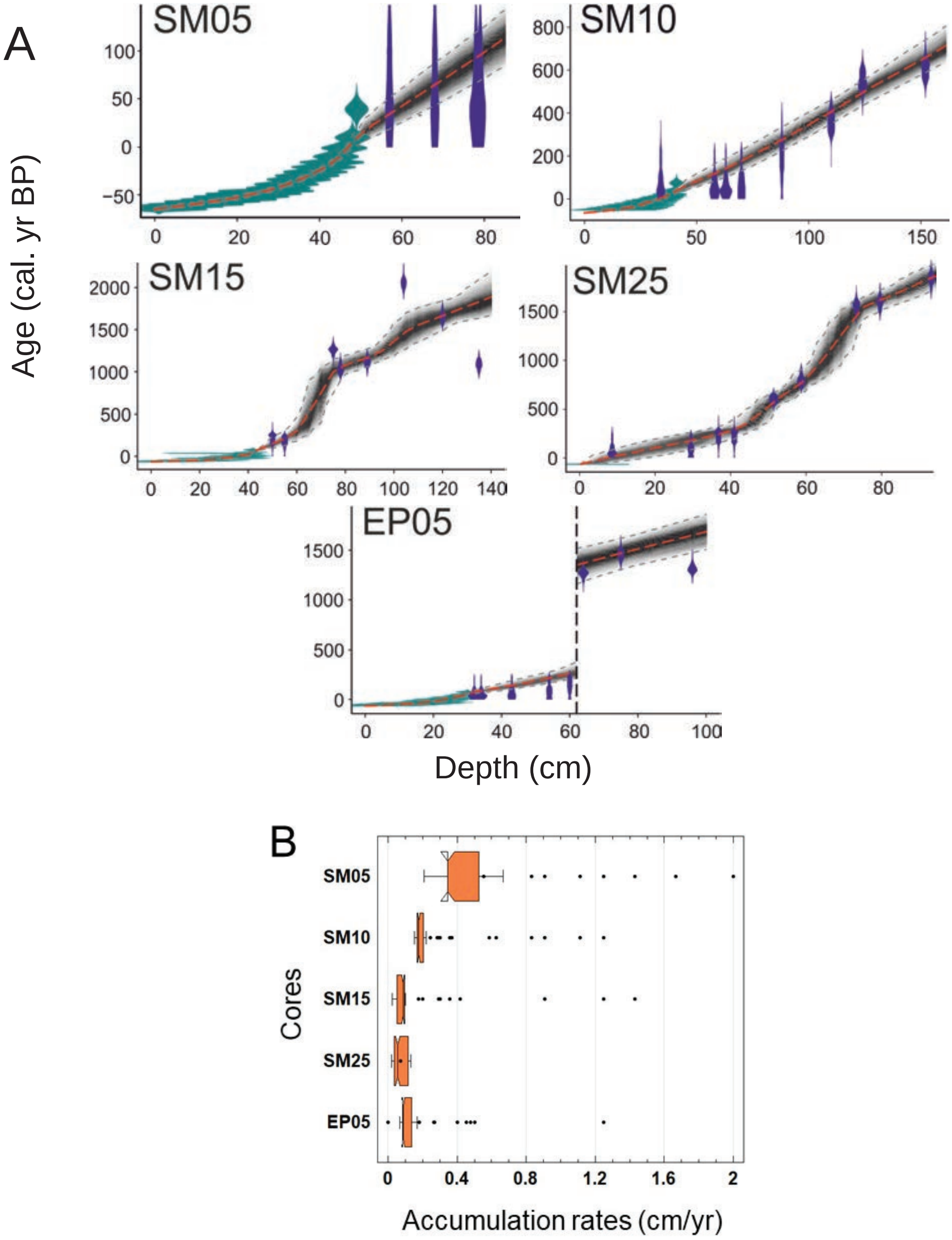

**Figure 3.** A) Bayesian age depth-models of Cabrera Island cores using Bacon.R software (Blaauw & Christen, 2011). Lead-210 (in green) and radiocarbon (in blue) dates were included in the age-depth models. Radiocarbon dates were calibrated using the *marine 13* calibration curve (Reimer et al., 2013) and corrected for a local marine reservoir effect (mean ± SD; ΔR = 26 ± 24 years; Riera Rullan, 2016). The red dashed curve shows the "best" model based on the weighted mean age for each depth. Individual radiocarbon dates are shown in probability density functions of calibrated ages. The grey area indicates the uncertainty envelope of the model with grey dashed curves indicating 95% confidence intervals. The vertical, dashed black line on the EP05 model denotes a hiatus. B) Notched box-plot of accumulation rates for each of the sampled cores.

**Table 3**. Radiocarbon dates in the *P. oceanica* mat cores retrieved at the Cabrera Island. The *marine 13* $^{14}$C calibration curve (Reimer et al., 2013) was used for calibration of the radiocarbon dates together with and a local marine reservoir effect (mean ± SD; ΔR = 26 ± 24 years; Riera Rullan, 2016).

| **Core** | **Laboratory code** | **Decomp. depth** (cm) | **AMS $^{14}$C date** (yr BP) | **Cal. yr BP** (2σ range) | **Weighted mean age** |
|---|---|---|---|---|---|
| **EP05** | D-AMS 014002 | 32 | 398 ± 23 | 58.5 – 92.4 | 75.8 |
| | D-AMS 019447 | 34 | 379 ± 24 | 66.7 – 108 | 87.1 |
| | D-AMS 014003 | 43 | 467 ± 27 | 104 – 190 | 141.3 |
| | D-AMS 012768 | 54 | 502 ± 27 | 166 – 277 | 215.4 |
| | D-AMS 029626 | 60 | 545 ± 30 | 202 – 349 | 263.6 |
| | D-AMS 019448 | 64 | 1741 ± 28 | 1185 – 1531 | 1369 |
| | D-AMS 012769 | 75 | 1940 ± 26 | 1305 – 1620 | 1468.9 |
| | D-AMS 012770 | 96 | 1788 ± 29 | 1473 – 1473 | 1651.6 |
| **SM05** | D-AMS 012771 | 57 | 75 ± 26 | 18.8 – 51.1 | 33.9 |
| | D-AMS 012772 | 68 | 105 ± 28 | 43.2 – 87.4 | 64.6 |
| | D-AMS 013117 | 78 | 366 ± 25 | 66.5 – 120 | 92.9 |
| | D-AMS 012773 | 79 | 439 ± 25 | 69.1 – 122 | 95.7 |
| **SM10** | D-AMS 019434 | 34 | 104 ± 25 | -0.9 – 7.2 | 3.2 |
| | D-AMS 019436 | 58 | 449 ± 28 | 83.9 – 163 | 117.6 |
| | D-AMS 019437 | 63 | 384 ± 29 | 103 – 138 | 141.1 |
| | D-AMS 019438 | 70 | 479 ± 26 | 130 – 228 | 177.1 |
| | D-AMS 022098 | 88 | 593 ± 61 | 225 – 334 | 275.2 |
| | D-AMS 022099 | 110 | 740 ± 34 | 348 – 462 | 405.6 |
| | D-AMS 022100 | 124 | 970 ± 45 | 434 – 551 | 494.6 |
| | D-AMS 022102 | 152 | 1063 ± 43 | 588 – 740 | 657.5 |
| **SM15** | D-AMS 019444 | 50 | 610 ± 24 | 89.4 – 242 | 151.8 |
| | D-AMS 012774 | 55 | 573 ± 23 | 126 – 305 | 207.6 |
| | UBA-32342 | 75 | 1732 ± 32 | 752 – 1154 | 996.7 |
| | D-AMS 019445 | 78 | 1508 ± 29 | 899 – 1169 | 1044.9 |
| | D-AMS 012775 | 89 | 1583 ± 23 | 1058 – 1269 | 1163.3 |
| | D-AMS 012776 | 104 | 2447 ± 32 | 1269 – 1703 | 1477.9 |
| | D-AMS 029627 | 120 | 2106 ± 29 | 1482 – 1845 | 1664.7 |
| | D-AMS 029628 | 135 | 1556 ± 29 | 1634 – 2098 | 1830.1 |
| **SM25** | D-AMS 019439 | 8 | 216 ± 46 | -49.5 – 63.9 | 7.3 |
| | D-AMS 014000 | 28 | 508 ± 20 | 76.7 – 243 | 165.3 |
| | D-AMS 019440 | 35 | 608 ± 27 | 144 – 303 | 229.2 |
| | D-AMS 014001 | 39 | 604 ± 29 | 181 – 383 | 271.8 |
| | D-AMS 012777 | 49 | 1000 ± 27 | 427 – 637 | 537.7 |
| | D-AMS 019441 | 56 | 1234 ± 27 | 628 – 852 | 728 |
| | D-AMS 012778 | 70 | 1957 ± 24 | 1170 – 1525 | 1374.6 |
| | D-AMS 019442 | 76 | 1985 ± 25 | 1428 – 1533 | 1532.2 |
| | D-AMS 012779 | 89 | 2178 ± 28 | 1619 – 1871 | 1748.5 |

**Table 4.** Factor loadings of the PCA$_{\text{pigments}}$ ran to explore potential associations in the community of primary producers as recorded by fossil pigment concentrations. Numbers in bold indicate pigments with highest factor loadings. Numbers in bold italics indicate pigments with moderate factor loadings.

| | **PC1$_{\text{pigments}}$** | **PC2$_{\text{pigments}}$** |
|---|---|---|
| Variance explained | 78% | 13% |
| Diadinoxanthin | **0.85** | -0.07 |
| Alloxanthin | 0.14 | -0.07 |
| Diatoxanthin | -0.18 | **0.55** |
| Lutein-zeaxanthin | ***-0.23*** | **0.49** |
| Canthaxanthin | ***-0.21*** | -***0.29*** |
| Echinenone | ***-0.37*** | **-0.59** |

### 3.1. Relationship between fossil pigment composition and environmental factors

A robust PCA explained 57% of the variance in fossil pigment composition using a combination of local and global predictive variables (Fig. 5A and Table 5). The first axis (PC1$_{\text{environmental}}$) accounted for 31% of the total variance and showed that diadinoxanthin was strongly and positively correlated with global climate indicators (TSI and NHT). Diadinoxanthin content was also moderately and positively correlated to $\delta^{13}$C, concentrations of chl-*a*, and the PPI. Echinenone and lutein-zeaxanthin abundances were also correlated moderately and negatively with diadinoxanthin (Fig. 5A).

PC2$_{\text{environmental}}$ accounted for 26% of the total variation (Fig. 5A). On this axis, abundances of diatoxanthin and lutein-zeaxanthin were positively correlated with chlorine, medium and fine-sands, PPI and chl-*a* content, while negatively correlated with echinenone and canthaxanthin. In contrast, echinenone and canthaxanthin were positively correlated with OM, $\delta^{15}$N, the BIT index, coarse-sandy fractions and β-carotene, and negatively with diatoxanthin and lutein-zeaxanthin (Fig. 5A and Table 5).

Overall, PC1$_{\text{environmental}}$ scores exhibited an increasing trend towards the present in most cores, in particular during the last 150-300 years (Fig. 5B). Temporal trends of PC2$_{\text{environmental}}$ scores showed no clear nor common pattern among cores through time, although they did show the same difference among embayments as described for PC2$_{\text{pigments}}$ (Fig. 5B).

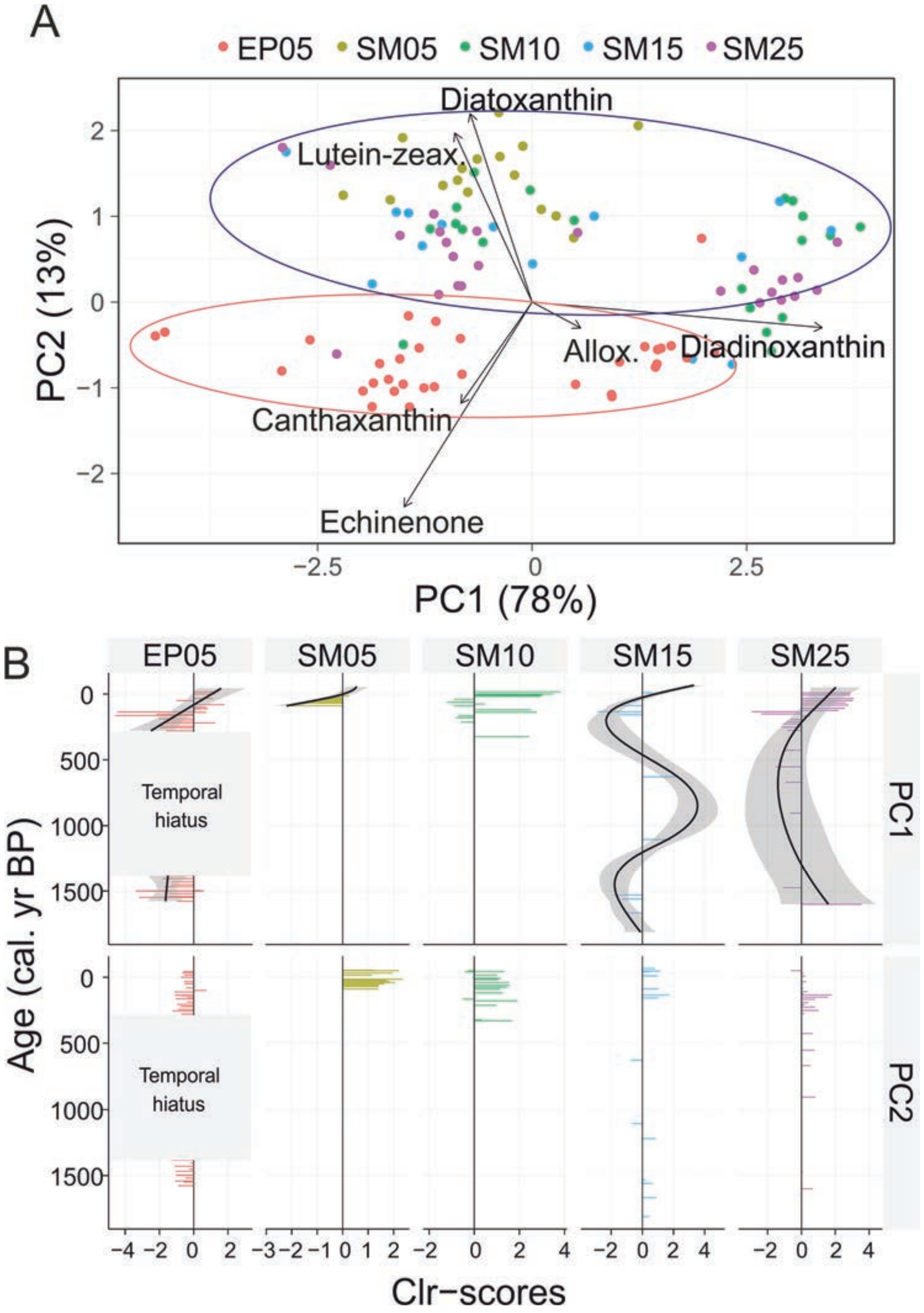

**Figure 4.** PCA$_{pigments}$ run to explore potential associations in the community of primary producers as recorded by fossil pigment concentrations in the cores. A) Clr-biplot of sample scores. Red ellipse indicates samples from EP and blue ellipse indicates samples from SM. B) Depth records of the PC$_{pigments}$ scores. Black solid lines indicate fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant trends are shown (p>0.05). Algal groups associated with pigments are in Table 3.

### 3.2. Dinocyst records

Dinocysts concentrations were low in sediments from both bays. They were 1-2 orders of magnitude higher in EP05 than in SM25 (Fig. 6). All dinocysts identified were of autotrophic affinity. In both bays, dinocyst concentrations were composed predominately of *Spiniferites* spp. and *Lingulodinium machaerophorum*. *L. machaerophorum* is the cyst produced by the motile form *Lingulodinium polyedrum*, a species which inhabits estuaries and coastal bays worldwide, including the Mediterranean Sea (Lewis & Hallett, 1997; Penna et al., 2006). The most notable feature of the dinocyst records is the presence of a trend towards increasing concentrations during the last two centuries, particularly for *Spiniferites* spp., *L. machaerophorum*, *Operculodinium* spp., and for total dinocysts (Fig. 6). These trends were significant only for EP05, which is perhaps related to the larger amount of samples processed in EP05 compared to SM25.

GAMs were employed to test if the temporal changes in concentrations of dinoflagellate pigment diadinoxanthin (as $PC1_{pigments}$ scores) were similar to those recorded for dinocysts (Fig. 7). Here the differences between the GAM-fitted pigments and cyst trends were estimated only for the most recent 250 yrs, the period during which there was directional change in fossil abundance in EP05. Comparisons were conducted between $PC1_{pigments}$ and total cyst concentrations (TC), as well as between $PC1_{pigments}$ and cysts from *Lingulodinium machaerophorum* (LM) and *Spiniferites* spp. (SS). Confidence intervals not encompassing zero, are indicative of significant differences between the smoothed trends (Rose et al., 2012). In EP05 core, no difference was observed between trends in any metric of cyst abundance (TC, LM or SS) and PC1 scores during the last 250 years (Fig. 7). Therefore, we infer that the increasing recent trend in $PC1_{pigment}$ and by inference the dinoflagellate biomarker diadinoxanthin mainly reflect changes in fossil concentrations of dinoflagellate cysts at least in the EP05 core (Fig. 6 and 7).

## 4. DISCUSSION

### 4.1. Seagrass phototrophic community

The overall composition of sedimentary pigments from the mat cores was consistent with the expected assemblage of primary producers observed in *P. oceanica* meadows. In general, modern macroalgal species are characteristically composed mainly of calcareous Rhodophyta and non-calcified Ochrophyta, whereas microalgal epiphytes usually include diatoms, dinoflagellates and cyanobacteria in declining relative abundance (Piazzi et al., 2016; Agawin et al., 2017).

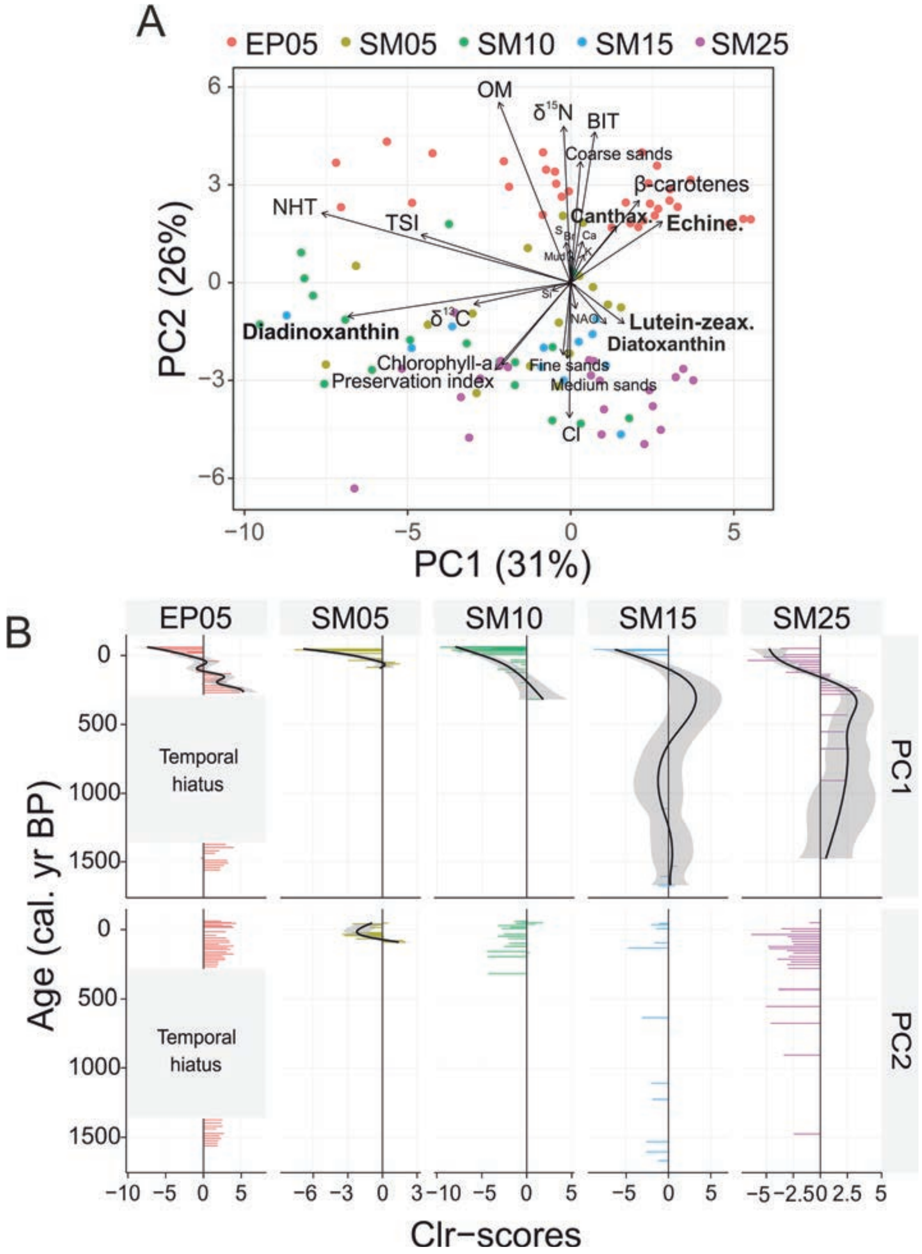

**Figure 5.** PCA$_{\text{environmental}}$ run to decipher relationships between fossil pigment composition and explicative variables: BIT index -an index of the relative abundance of terrestrial organic matter versus marine input in marine sediments (Hopmans et al., 2004), Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012), Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013), grain-size distribution, content of organic matter (OM), XRF-measured elements (Fe, Si, Ti, K, Ca, S, Cl and Br), carbon and nitrogen stable isotopes, chl-*a* and β-carotenes, and a pigment preservation index (chl-*a*/pheophytin *a*). **A)** Clr-biplot of sample scores. **B)** Depth records of the PC$_{\text{environmental}}$ scores. Black solid lines indicate fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant trends are shown ($p > 0.05$). Algal groups associated with pigments are in Table 3.

**Table 5.** Factor loadings of the $\text{PCA}_{\text{environmental}}$ ran to decipher relationships between marker pigment composition and explicative variables. Numbers in bold indicate variables with the highest factor loadings and in bold. Numbers in bold and italics indicate variables with moderate factor loadings. Explicative variables are the Branched and Isoprenoid Tetraether (BIT) index -an index of the relative abundance of terrestrial organic matter versus marine input in marine sediments (Hopmans et al., 2004)-, Total Solar Irradiance (TSI, Vieira et al., 2011), index of North Atlantic Oscillation (NAO, Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012), Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013), grain-size distribution, content of organic matter (OM), XRF-measured elements (Fe, Si, Ti, K, Ca, S, Cl and Br), carbon and nitrogen stable isotopes, chl-*a* and β-carotenes, and a pigment preservation index (chl-*a*/pheophytin *a*).

| | **$\text{PC1}_{\text{environmental}}$** | **$\text{PC2}_{\text{environmental}}$** |
|---|---|---|
| Variance explained | 31% | 26% |
| Diadinoxanthin | **-0.53** | -0.08 |
| Alloxanthin | -0.01 | 0.00 |
| Diatoxanthin | 0.08 | -0.10 |
| Lutein-zeaxanthin | 0.13 | -0.10 |
| Canthaxanthin | 0.11 | ***0.13*** |
| Echinenone | ***0.22*** | ***0.14*** |
| β-carotenes | ***0.16*** | ***0.19*** |
| chl-*a* | ***-0.16*** | ***-0.19*** |
| Mud | 0.00 | 0.06 |
| Fine sands | -0.02 | ***-0.17*** |
| Medium sands | -0.01 | ***-0.18*** |
| Coarse sands | 0.02 | **0.29** |
| Gravel | 0.00 | 0.00 |
| Si | -0.04 | -0.02 |
| S | -0.01 | 0.10 |
| Br | 0.00 | 0.08 |
| Cl | 0.00 | **-0.32** |
| K | 0.03 | 0.07 |
| Ca | 0.03 | 0.10 |
| Ti | 0.00 | 0.00 |
| Fe | 0.00 | 0.00 |
| TSI | **-0.35** | 0.11 |
| NAO | 0.01 | -0.06 |
| NHT | **-0.59** | 0.16 |
| BIT | 0.06 | **0.36** |
| $\delta^{13}C$ | ***-0.23*** | -0.05 |
| $\delta^{15}N$ | -0.02 | **0.37** |
| OM | ***-0.17*** | **0.43** |
| Preservation index | ***-0.18*** | **-0.21** |

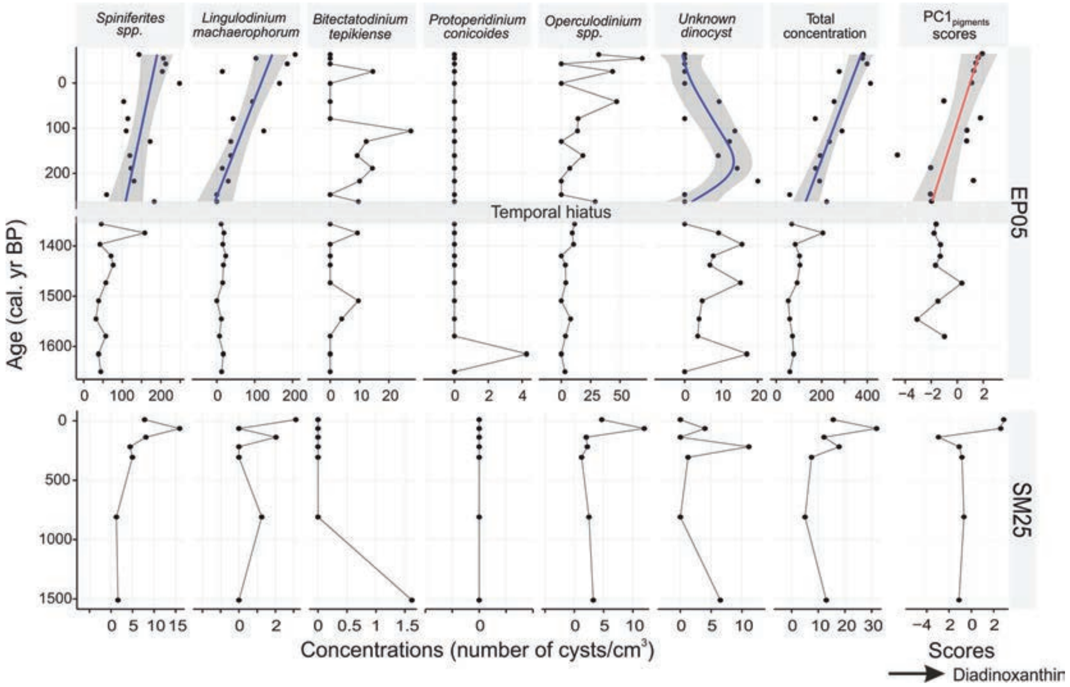

**Figure 6.** Dinocyst concentrations records of cores EP05 and SM25 plotted together with PC1$_{\text{pigments}}$ scores. Positive scores of PC1pigments are related to higher concentrations of diadinoxanthin. Coloured solid lines indicate fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant trends are shown (p > 0.05).

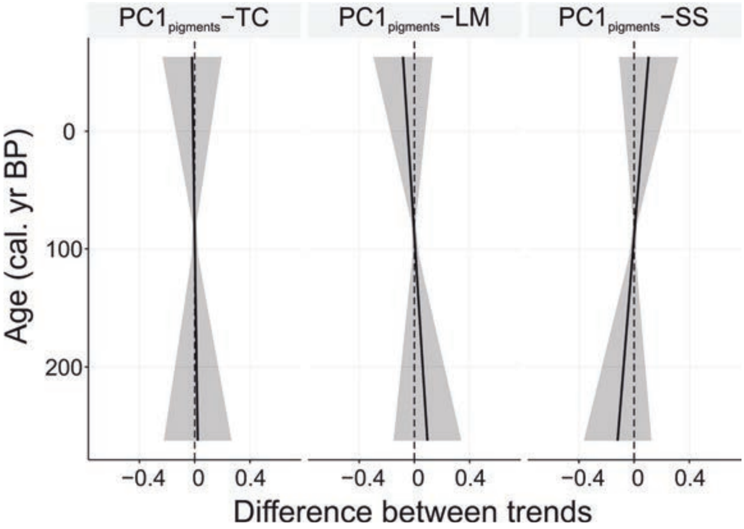

**Figure 7.** Differences between fitted trends in the scores of PC1pigments and dinocysts records for the last 250 years in EP05. Black solid lines indicate differences between fitted smooth functions of time (GAM models, formula = y ~ s(x)) of PC1pigments scores, concentrations of total dinocysts (TC), *Lingulodinium machaerophorum* (LM) and *Spiniferites* spp. (SS). Grey shaded regions are 95% point-wise confidence intervals on these differences.

Similarly, the modern phytoplankton assemblages are mainly composed of diatoms and dinoflagellates (Moncer et al., 2017), while the water column near Cabrera is known to harbour a great abundance of pico and nanoplankton, dinoflagellates, coccolitophorids and diatoms (Vives, 1993). We suggest that seagrass, possibly in association with rhodophytes, is the main source of the couplet lutein-zeaxanthin, as it is the most abundant carotenoid in live *P. oceanica* tissues (Casazza & Mazella, 2002).

### 4.2. Observed temporal and spatial patterns

Multivariate analysis of the cores revealed two main patterns of change in the fossil pigment assemblages. First, we recorded a temporal shift in the abundance of dinoflagellates and siliceous algae, which appears to reflect the influence of global climate change, particularly the inputs of energy as irradiance and heat (i.e., TSI and NHT). Second, our results showed clear spatial patterns in primary producers' community composition, seemingly related to embayment-specific local conditions (EP *versus* SM), and to the water depth gradient (SM gradient). Taken together, these patterns suggest that primary producers in seagrass meadows are influenced by a combination of global and local regulatory mechanisms.

#### The recent increase in dinoflagellates

Increased abundance of dinoflagellates and possibly siliceous taxa (as the carotenoid diadinoxanthin) was observed among all cores over the last 150-300 years (Fig. 4 and 5). Our results suggest that the carotenoid diadinoxanthin was more abundant during episodes of high solar irradiance (i.e., TSI), air temperature (i.e., NHT) and, to a lesser extent, ecosystem production (i.e., $\delta^{13}C$ and chl-*a*) according to $PC1_{environmental}$ (Fig.5A). Hence, changes in dinoflagellate abundance seem to be influenced by global climate variables - specifically the input of energy as irradiance and heat. Changes in pigment preservation may also partly explain these historical trends, as noted with the direction of the pigment preservation index vector (Fig. 5A). Post-depositional degradation may contribute to the decline in labile diadinoxanthin with increasing sediment age ($PC1_{pigments}$ and $PC1_{environmental}$, Fig. 4B and 5B). However, analysis of resting cysts from dinoflagellates in cores EP05 and SM25 also showed an increase in dinoflagellate abundance over the same period, especially for *L. machaerophorum* and *Spiniferites* spp. in EP05 (Fig. 6). Dinocysts are composed of highly resistant organic compounds, which are preserved well in sediments (Versteegh & Blokker, 2004). Given the strong concordance between historical trends in the dinoflagellate biomarker diadinoxanthin (as $PC1_{pigments}$) and dinoflagellate cyst concentrations, we infer that increased abundance of diadinoxanthin over the past ~250 years reflects actual changes in algal biomass, rather than slow post-depositional degradation in the *Posidonia* seagrass mats.

The observed orthogonal relationship between diadinoxanthin and diatoxathin in the two PCAs was unexpected because both pigments usually co-occur in several algal groups, as in diatoms and dinoflagellates. Although speculative, this lack of correlation could be due to the fact that they are associated with different algal groups in the particular setting of Cabrera: diadinoxanthin with dinoflagellates and diatoxanthin with diatoms. Regardless, the uncorrelated nature of historical trends in diadinoxanthin and the diatom-specific biomarker diatoxanthin again suggests that historical trends in diadinoxanthin were recording mainly changes in marine dinoflagellate abundance.

Increased abundance of dinoflagellates during periods of elevated solar irradiance may be related to their ability to produce substantial amounts of UV-absorbing photo-protective compounds under high irradiance (Hannach & Sigleo, 1998). In this sense, diadinoxanthin is known to act as a photoprotective accessory pigment (Lavaud et al., 2002; Laviale & Jacques, 2011). Diadinoxanthin is not only present in dinoflagellates but also in some species of raphidophytes (e.g., *Heterosigma akashiwo, Chattonella subsalsa)*, which also thrive in high UV environments (Fu et al., 2012; Wells et al., 2015). Similarly, elevated water temperature may favour growth of epiphytic dinoflagellates and diatoms in seagrass meadows (Johnson et al. , 2005; Turki, 2005; Frankovich et al., 2006; Mabrouk et al., 2012). Moreover, the correlation between dinoflagellates and temperature found here was also described in several long-term dinocyst records, in which high *L. machaerophorum* and *Spiniferites* spp. abundance correlated with warmer sea surface waters and stronger stratified conditions in coastal areas (Pospelova et al., 2006; Sobrino et al., 2012; Bringué et al., 2013; Leroy et al., 2013). Those studies also reported sharp increases in *L. machaerophorum* over the last century, similar to the patterns observed in this study (Fig. 5A). *L. machaerophorum* is also a potentially-toxic taxon, known to produce yessotoxins (e.g. Paz et al., 2004; Armstrong & Kudela, 2006). Therefore, their higher abundance could increase the risk of toxic algal blooms that could affect the entire ecosystem composition and structure (Sellner et al., 2003).

Our results provide a predictive understanding of the response of phototrophic assemblages in seagrass meadows to global change. Specifically, we anticipate an increase in dinoflagellates as a consequence of global warming. The exact consequences of this change in the composition of primary producers are so far unknown. Our study points to a greater contribution of autotrophic dinoflagellates to autotrophic production in seagrass meadows, possibly leading to the outcompetition of the seagrass (Fig. 5A). Providing dinoflagellates do not outcompete the seagrass and go through mass encystment, they could even have an effective contribution to carbon sequestration (Spilling et al., 2014; Wasmund et al., 2017). However, the latter speculation may be difficult to evaluate, as *P. oceanica* is thought to be negatively impacted by the on-going sea water warming (Marbà & Duarte, 2010; Savva et al., 2018).

### Spatial differences between bays and along water depth

Our results revealed pronounced spatial patterns in primary producer community composition, caused by site-specific local effects, as well as the natural depth gradient. In the anthropogenically-impacted EP setting, the community was mainly dominated by cyanobacteria (as canthaxanthin and echinenone), whereas diatoms (as diatoxanthin), chlorophytes, rhodophytes and, most probably, the seagrass (all as lutein-zeaxanthin) were more characteristic of the less disturbed SM setting. As detailed below, these patterns may arise because of basin-specific differences in local land use and catchment characteristics, specifically nutrient and terrestrial organic matter inputs.

The cyanobacteria-rich community of EP developed in an environment with elevated organic matter and nutrient inputs, mainly of terrestrial origin (high loadings for BIT index, $\delta^{15}$N and OM in PC2 $_{\text{environmental}}$, Fig. 5). In EP, higher microbial decay would also explain the $\delta^{15}$N enriched sediment organic matter relative to that of SM (Craine et al., 2015). Aside from high nutrient availability, EP waters have other physical conditions favourable to elevated cyanobacterial abundance compared to SM, such as longer water residence times and enhanced stratification (Orfila et al., 2005; Paerl & Huisman, 2008). On the other hand, diatoms, the seagrass and likely, rodophytes prevailed in SM (Fig. 4A), where organic matter is mainly derived from marine autochthonous production, as indicated by a high loading for chlorine in PC2$_{\text{environmental}}$ (Fig. 5A), an element known to be incorporated in labile marine organic matter (Leri et al., 2015). Our findings support those of Holmer et al. (2003, 2004) who reported an organic enrichment and higher mineralization rates in EP, as well as a significantly higher net community production in SM, reflecting higher light availability, lower terrestrial inputs and higher water turnover rates.

Studies of phytoplankton communities in marine waters have observed increases in the abundance of cyanobacteria under ammonium enrichment, whereas diatoms more commonly bloom when exposed to elevated nitrate concentrations (Berg et al., 2003; Heil et al., 2007; Glibert et al., 2014). Cyanobacteria are generally considered specialists that have a superior ammonium uptake kinetics (Blomqvist et al., 1994; Lindell & Post, 2001). Further, cyanobacteria can use organic matter as a nitrogen source in both lakes and marine ecosystems (e.g., Berman, 2001; Sakamoto & Bryant, 2001; Berg et al., 2003; Glibert et al., 2004; Donald et al., 2011). Therefore, the predominance of cyanobacteria in EP could reflect an elevated influx of ammonium or other N species as a result of the enhanced organic matter decomposition in this bay (Holmer et al., 2004; Pérez et al., 2007), or higher availability of dissolved organic matter. The naturally high organic matter accumulation in EP arises from discharges of the main pluvial network of the island (Rodríguez-Perea & Servera, 1993), and from the longer water residence time in EP, which, together, may favour particle sedimentation and a larger contribution of allochthonous organic matter to the bottom deposits. In fact, Mazarrasa et al. (2017a) observed that allochthonous carbon accounted for more carbon in meadows from EP than in other Balearic meadows, including SM.

At SM shallowest station (SM05, Fig. 4A), pigment assemblages indicated dominance of diatoms (diatoxanthin), seagrasses, and rhodophytes (lutein-zeaxanthin) compared to the deeper stations. A greater abundance of diatoms in the shallowest areas could be related to the diatoms' feature of developing better in turbulent, well-mixed waters (Mabrouk et al., 2011). The greater abundance of seagrass at shallower depths could be explained by higher light availability and, therefore, higher photosynthetic rates and production (Alcoverro et al., 2001b). In general, water depth is a key regulator of epiphytes assemblages of seagrasses due to differences in the seagrass and meadow structural characteristics, light penetration, and hydrodynamics (Piazzi et al., 2016 and references therein).

## 5. CONCLUSIONS

The use of fossil pigments is feasible in sheltered vegetative coastal habitats. In this sense, this study pioneers in the use of fossil pigments in *P. oceanica* mats as proxy of phototrophs composition. Fossil pigments can be used in *Posidonia* spp. meadows, where chronologically ordered sequences are highly preserved in the sediments below them (i.e. the mats), but it could also be used in other smaller seagrass located in sheltered areas where sedimentation is not altered.

Our results report changes in phototrophic community composition and production in *P. oceanica* meadows at centennial scales. Analyses suggest that these changes were modulated by both local terrestrial influences and global climate factors. In particular, elevated solar irradiance and air temperature seem to have driven increases in dinoflagellates abundance over the last 150-300 years. Local environmental conditions were most likely responsible for differences in phototrophic communities between basins; apparently due to differences in terrestrial organic matter and nutrient inputs. Depth also influenced the phototrophic community composition, with a greater predominance of pigments from diatoms, seagrasses and rodophytes in shallower waters.

These patterns confirm that primary producers in seagrass meadows are under complex hierarchical control by local and global regulatory mechanisms and provide better insights into potential phototrophic responses to global change. Specifically, we infer that global warming may favour the development of autotrophic dinoflagellate assemblages, which could negatively affect the ecosystem functioning by shading and outcompeting the seagrass. Future research could focus on the potential effects of these structural community changes on seagrass ecosystem functioning under predicted climate change scenarios.

## APPENDIX[2]

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[2] See supplementary materials in Appendix B.

# CHAPTER

# 3

# LONG-TERM DYNAMICS OF PRODUCTION IN WESTERN MEDITERRANEAN SEAGRASS MEADOWS: TRADE-OFFS AND LEGACIES OF PAST DISTURBANCES

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# ABSTRACT

Seagrasses are marine angiosperms that can form highly productive, and valuable underwater meadows, which are currently in regression. A reliable assessment of their status and future evolution requires studies encompassing long-term temporal scales. With the aim of understanding seagrass ecosystem dynamics over the last centuries and millennia, twelve sediment cores were studied from seagrass meadows located along the Andalusian coast and at the Cabrera Island (western Mediterranean). This study is pioneer in using Fourier Transform Infrared (FTIR) spectroscopy as a tool to study environmental change in seagrass sediments. FTIR is a form of vibrational spectroscopy that provides information about the sediment chemical composition. Principal Component Analysis (PCA) was used to summarise spatio-temporal data of the FTIR vibratory peaks in combination with climate and geochemical proxy data. Several PCA signals were identified: (1) one likely related to the relative changes of the main primary producers and the sedimentary environment (carbonate or siliciclastic sediments, with aromatic or aliphatic organic matter); (2) the marine community production (polysaccharides, total organic matter content and biogenic silica); and (3) the seagrass production (aromatics, carbohydrates, phenols, proteins and lipids). A decrease of seagrass production along the mainland coast was evident since AD ~1850, which may be due to combined negative impacts of seawater warming, local anthropogenic impacts, and extreme setting conditions. The legacy of these combined stressors might have influenced the current poor state of seagrass meadows in the Alboran Sea. Our results also revealed a significant long-term trade-off between the level of seagrass production and its temporal stability (calculated as the inverse of the coefficient of variation). This study provides a reliable baseline data, helping to assess the magnitude of seagrass regression and its drivers. This paleoecological information can help design more targeted management plans and identify meadows where local management could be more efficient.

# 1. INTRODUCTION

There is growing concern over the constant loss of coastal ecosystems because they are among the most productive ones with fundamental processes and functions that provide a wide range of benefits to our societies (Alongi, 2002; Hoegh-Guldberg et al., 2008; Waycott et al., 2009). With the pressure of more than one-third of the world's population inhabiting coastal areas, these habitats are showing regressive trends worldwide as a consequence of local anthropogenic disturbances but also of global climate change (Millennium Ecosystem Assessment, 2005; Lotze et al., 2006; Baker et al., 2008; Davidson, 2014).

Seagrasses are marine plants that form extensive underwater meadows, one of these highly productive and threatened coastal ecosystems experiencing global loss during the 20th century (e.g. Duarte, 2002; Orth et al., 2006a; Waycott et al., 2009). Their regression, although spatially variable (Waycott et al., 2009; Telesca et al., 2015), is especially worrying in the Mediterranean Sea, where seagrass meadows are the most relevant coastal habitats considering their abundance and ecological value (Ruiz-Fernandez et al., 2009; Telesca et al., 2015). The main seagrass species distributed along the Mediterranean Sea are *Cymodocea nodosa* (Ucria) Ascherson, and the most abundant and endemic species *Posidonia oceanica* (L.) Delile. Since the second half of the 20th century, a declining trend has been observed for the areal extent, cover and shoot density of *P. oceanica* (Marbà et al., 2014). The regression was found not only in areas under intense anthropogenic pressure but also in relatively pristine environments (Marbà et al., 2005; Marbà & Duarte, 2010). The main drivers behind *P. oceanica* loss are considered to be water quality degradation, mechanical damage, coastal modification and extreme events that could be related to global climate change, in order of importance (de los Santos et al., 2019).

However, the evaluation of seagrass trends and the plausible causes of change are based on the observational record that began in AD ~1870 (e.g. Boudouresque et al., 2009; Marbà et al., 2014; de los Santos et al., 2019), and does not allow for a proper assessment of the role and magnitude of the present climate forcing. Paleoenvironmental reconstructions can provide a baseline of the ecosystem status previous to the onset of recent anthropogenic activities (i.e. industrial era), indicating as well how the ecosystem responded to past natural changes. Long-term information on ecosystem dynamics can greatly increase the success of conservation and management plans by providing a framework within which we can evaluate present and plausible future trends (Oldfield & Dearing, 2003).

Paleoecological studies are of special interest in *P. oceanica* meadows. This species is the largest but also one of the slowest growing with a very slow recovery as well; therefore, substantial changes and responses manifest over long time scales of decades to centuries (Duarte et al., 2006; Kilminster et al., 2015). Fortunately, these ecosystems form environmental archives below the meadows, which can persist for thousands of years and enable a paleoecological approach (Mateo et al., 1997, 2002; Serrano et al., 2016b; López-Merino et al., 2017; Lafratta et al., 2018). To date, most of the seagrass paleoreconstructions have been limited to the local scale, using only one or few sediment records for the local area of interest. However, a multi-core paleoecological approach, with well-dated sediment records from several sites distributed along a region can provide a deeper and more reliable understanding of long-term processes, dynamics and drivers of change at a larger spatial scale (e.g. Reavie & Baratono, 2007; Wiklund et al., 2017). This is especially crucial in seagrass ecosystems to comprehend the spatial differences in their decline along the western Mediterranean coast (Marbà et al., 2005, 2014).

*Posidonia oceanica* forms environmental archives, also known as mats, mainly composed of organic material from all the organisms that inhabit the meadow and the overlying water column, but especially from the decay-resistant seagrass tissues, all trapped and accumulated over millennia (e.g., Kaal et al., 2016; Mazarrasa et al., 2017a). The organic material is integrated in an inorganic matrix, which can have a biogenic (*in situ* biologically precipitated carbonates) or lithogenic origin (erosion of coastal catchment soils) (Mateu-Vicens et al., 2012; Gaglianone et al., 2017).

The field of paleoecology in seagrass ecosystems has been gradually increasing and studies have based their results on a wide range of biotic and abiotic proxies. Some of the studied proxies are quite specific such as pollen (López-Sáez et al., 2009; López-Merino et al., 2015, 2017) or metal content of seagrass debris and sediment (Serrano et al., 2011, 2013, 2016b). However, other proxies used in seagrass paleoreconstructions are more common, like sediment organic carbon and nitrogen elemental and isotopic composition, carbonates content and grain-size distribution (Macreadie et al., 2015; Marbà et al., 2015; Serrano et al., 2016c; Mazarrasa et al., 2017a, 2017b; Leiva-Dueñas et al., 2018). However, to date, techniques providing information about more specific sediment organic and inorganic composition have not yet been used in seagrass paleoreconstructions. Infrared spectroscopy (IR) is a non-destructive analytical method that can be used for a qualitative and, when properly calibrated, quantitative identification of major changes in multiple organic and inorganic compounds across sediment layers. This technique is based on the stimulation of molecular vibrations by infrared radiation, molecular vibrations that depend on the structural, chemical bonds of the compounds. The large amount of information on inorganic and organic substances provided from each sample in a single measurement, the fact that is a fast and low-cost technique, with simple sample pre-treatments, and requiring very small amounts of sample material (< 1 g) makes of this technique a tool of great potential in multi-proxy paleoecological studies (e.g. Chang et al., 2005; Vogel et al., 2008; Rosén et al., 2009, 2010; Meyer-Jacob et al., 2014; Van de Broek & Govers, 2019), as well as for assessing the ecosystems health status (Artz et al., 2008). It has even been recently applied to quantitatively determine charcoal and microplastic content in bulk sediment samples (Cadd et al., 2019; Hahn et al., 2019). However, the potential of IR spectroscopy to reconstruct paleoecological processes through relative changes in seagrass sediment compounds has yet to be explored. By elucidating the associations between the characteristic wavenumbers of Fourier transform infrared (FTIR) spectra and the compounds in seagrass sediments, our study can also set the basic knowledge needed for future investigations aiming to use FTIR for accurate quantitative estimation of main seagrass sediment components such as organic and inorganic carbon, biogenic silica, and mineralogical composition (e.g. quartz and feldspars).

Considering the potential information that can be obtained using FTIR in coastal sediments, in this study, we aim at reconstructing long-term processes and dynamics of seagrass meadows along the Mediterranean Spanish coast using a multi-core and multi-proxy approach with FTIR spectroscopy and other sedimentological proxies. The specific objectives are: (1) to evaluate the potential of FTIR spectroscopy for identifying the main organic and inorganic components in seagrass mats, in order to reconstruct the main ecological processes associated with seagrass meadows functioning; (2) to determine the variability of these processes over time and across spatial gradients, and; (3) to identify the long-term environmental drivers which may regulate the main ecological processes in the meadows studied.

## 2. MATERIALS AND METHODS

### 2.1. Environmental setting and coring procedures

Seagrass meadows were sampled in the western Mediterranean, along the Andalusian coast (south continental Spain), and in two bays of the Cabrera Island, the largest island of the Cabrera Archipelago (south of Balearic Islands) (Fig. 1). All cores come from *P. oceanica* meadows, except core BA, which was collected from a *C. nodosa* meadow (core BA, Table 1). Seagrass meadows in Cabrera grow on biogenic, carbonate-rich, and iron-deficient sediments, while in Andalusia, they grow on more terrigenous sediments (Marbà et al., 2005).

The climate along the Andalusian coast is subdesertic Mediterranean in the easternmost area, where the study sites RO, BA, AG, DE, and TE were located (mean annual temperature of 17.6 ºC) and subtropical in the western area, where the study sites CA and ME are found (mean annual temperature of 17.2 ºC; 1961-2000; CAGPDS, 2014). Precipitation in the western Andalusian area is more abundant (719 mm) and uniform than in the eastern area (236 mm; Liquete et al., 2005; CAGPDS, 2014).

The climate in the Cabrera archipelago is semi-arid with a mean annual temperature of 14.6 ºC and precipitation of 375 mm during the period 1950-1971 (Alcover et al., 1993). Terrestrial sediment supplies to coastal areas take place mainly under heavy episodic rainfalls. Liquete et al. (2005) proved that Andalusian river systems are quite efficient in terms of sediment delivery despite the small size of their catchments.

The Alboran Sea (where CA, ME, RO, and BA are located) is an area that shows a very high primary productivity, with cold waters, and elevated concentrations of Chl *a* mainly due to upwelling events. The high productivity in the Alboran sea is due to upwelling of nutrient-rich deeper waters. These upwellings can be wind-induced but also happen along the edges of the anticyclonic gyres of the Alboran Sea (Garcia-Gorriz & Carr, 2001). In contrast, the eastern side (where AG, DE, and TE are located) has warmer waters with lower Chl *a* content (Ramírez et al., 2005; Muñoz et al., 2015).

Due to the increasing water nutrient content, turbidity is also higher towards the west. As a consequence, seagrasses grow at shallower depths and form patchier meadows the more to the west along the Andalusian coast (CAGPDS, 2018). Coastal waters surrounding the Cabrera archipelago have a very low nutrient content compared to other coastal Mediterranean waters (Ballesteros & Zabala, 1993). In fact, a trophic gradient is observed from the southwest to the northeast in the Spanish Mediterranean waters, with decreasing nutrient and chlorophyll concentrations northeastward (del Carmen García-Martínez et al., 2019). Seagrass meadows along the Iberian coast compared to those in Cabrera Island showed a higher reliance on local sources of dissolved inorganic nitrogen pools (Papadimitriou et al., 2005), while meadows located in Cabrera Island seemed to depend more on atmospheric nitrogen (Garcias-Bonet et al., 2016).

Population density and human impacts are and have been greater along the Andalusian coast compared to the Cabrera island. Denser populated areas are located in the western side of Andalusia, although some considerable urban areas also exist in the eastern side, near our study sites DE and TE. Artisanal fisheries and nautical sports activities are the main impacts in Andalusia. ME is located in a meadow where impacts from illegal wastewater discharges,

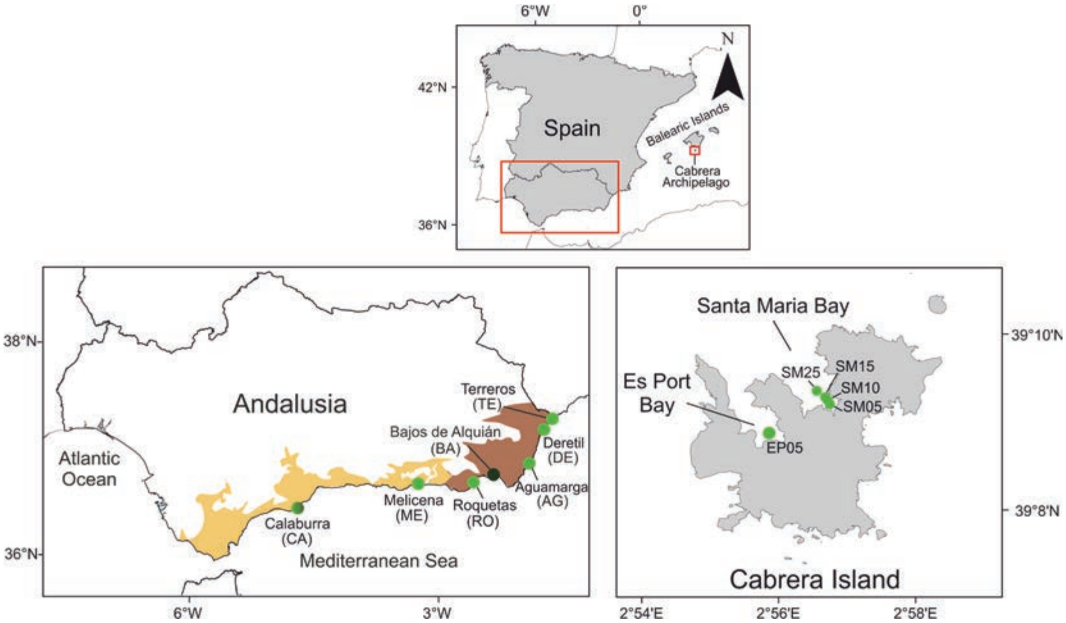

**Figure 1.** Location of the seagrass sediment cores. Circles indicate sampling sites. Light green-coloured: *P. oceanica* meadows; Dark green: *C. nodosa* meadows. The numbers in Santa Maria Bay stand for the sampling depth (in meters). In Andalusia we can see the two bioclimatic regions affecting our sampling sites, they are coloured in light orange (subtropical Mediterranean) and light brown (subdesertic Mediterranean).

**Table 1**. Sampling sites details. Comp. (%) stands for the mean degree of compression of each core, calculated as specified in the supplementary material. Mediter. stands for Mediterranean.

| **Region /Province** | **Location** | **Coordinates** | | **Water depth** (m) | **Seagrass species** | **Code** | **Core length** (cm) | **Comp.** (%) |
|---|---|---|---|---|---|---|---|---|
| Alboran, Málaga | Calaburras | 36°29'25.9"N | 4°41'37.25"W | 0.5 | *P. oceanica* | **CA** | 103 | 12.6 |
| Alboran, Granada | Melicena | 36°44'53.99"N | 3°14'3.78"W | 4.2 | *P. oceanica* | **ME** | 78 | 22.3 |
| Alboran, Almeria | Roquetas | 36°47'15.50"N | 2°35'20.10"W | 1.5 | *P. oceanica* | **RO** | 140 | 41.6 |
| Mediter., Almería | El Alquian | 36°49'39.1"N | 2°23'14"W | 6.8 | *C. nodosa* | **BA** | 117 | 9.8 |
| Mediter., Almería | Aguamarga | 36°56'15.66"N | 1°56'0.42"W | 4.8 | *P. oceanica* | **AG** | 173 | 13.1 |
| Mediter., Almería | Villaricos | 37°15'18.93"N | 1°45'29.53"W | 16 | *P. oceanica* | **DE** | 157 | 16 |
| Mediter., Almería | Terreros | 37°21'0.12"N | 1°40'36.37"W | 5.5 | *P. oceanica* | **TE** | 88 | 14.3 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39º9'0"N | 2º56'57"E | 5 | *P. oceanica* | **SM05** | 83 | 42 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39º9'3"N | 2º56'55"E | 10 | *P. oceanica* | **SM10** | 161 | 18 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39º9'6"N | 2º56'53"E | 15 | *P. oceanica* | **SM15** | 138 | 19 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39º9'12"N | 2º56'44"E | 25 | *P. oceanica* | **SM25** | 89 | 5.6 |
| Mediter., Cabrera Archipelago | Es Port Bay | 39º8'42"N | 2º55'60"E | 5 | *P. oceanica* | **EP** | 98 | 17 |

trawling and *small*-scale fisheries have been observed. The study sites RO and DE are currently the most impacted meadows. RO is under multiple human pressures, such as urban wastewaters, massive tourism, mooring, trawling, and dredging. The meadow of DE has been subjected to chemical wastewater discharges since the late 1960s and is profoundly impacted, having lost the seagrass cover between its upper limit and a depth of 10-12 m (Moreno et al., 1999, 2001). The impact has been observed despite a wastewater treatment plant installed in 1999 (CMAOT, 2014). The Cabrera Island became part of a Spanish National Marine Park in 1991. There has never been a high permanent population in the island (<50 people; Frontera et al., 1993). The overall environmental conditions of the meadows in the Cabrera island are more pristine. This is especially the case in SM Bay, currently closed to visitors and with a healthy, dense, and continuous meadow until 37 m depth. However, the meadow at EP Bay is less productive and shows higher mortality rates (Marbà et al., 2002; Holmer et al., 2003). This bay receives hundreds of visitors each summer, also allowing the access to ~50 ships a day, which discharge their raw wastewaters into the bay waters (Marbà et al., 2002). The historical population of the island has been settled around EP Bay (e.g. Orfila et al., 1992), because the few arable lands were nearby (Riera Rullan, 2016). Moreover, this bay has been used as a natural harbour, providing important refuge from winds and storms (Dawson, 2013). Therefore, anthropogenic impacts in the island are and have been mainly concentrated in EP Bay.

Sediment coring was conducted in June 2015 in the Cabrera Island and in October 2016 and July 2017 along the Andalusian coast. Most cores were collected at depths ranging between 0.5 and 10 m except for a transect at 5, 10, 15, and 25 m depth in Santa Maria Bay (SM, Cabrera) (Table 1). One core was retrieved per location of study except for SM Bay, where four cores were obtained along the previous water-depth transect. Cores were collected by SCUBA divers, who manually, gently hammered and rotated high-density PVC tubes (1 and 1.5 m long and 7 cm internal diameter) into the soil. These tubes had core catchers fitted at the bottom to avoid the loss of sediment during retrieval and a serrated leading edge to favour the penetration. The empty space at the top of the core was filled with Styrofoam and then capped with a plastic tap. A bottom cap was also placed after pulling the core out of the sediment. Divers kept the core tubes vertical at all times. An exponential decompression function was applied to correct for core shortening (Morton & White, 1997; Serrano et al., 2012).

## 2.2. Laboratory analyses

Cores were cut longitudinally and opened into two halves. One-half of each core was analysed non-destructively for elemental composition using a model Avaatech XRF core scanner at CORELAB laboratory (University of Barcelona). Most of the cores were cut into 1 cm-thick samples except CA and ME (Table 1), which were cut into 2 cm-thick slices. Alternate samples were dried at 60ºC until constant weight to determine dry bulk density. Before grinding, organic seagrass debris larger than 2 mm (after sieving) were picked and weighted to obtain the coarse seagrass organic matter content (seagrass COM), and then returned to its sample, which was then homogenised using an agate mortar (Mortar Grinder RM-200 RETSCH).

The organic matter content was estimated by mass-loss-on-ignition at 450ºC for 5h. Carbon and N elemental and isotopic composition of sediment samples were analysed on a Thermo-Finnegan Delta V IRMS isotope ratio mass spectrometer coupled with a Costech elemental analyser at UH Hilo Analytical Laboratory (University of Hawaii at Hilo).

FTIR spectra of the ground sediment samples were obtained using an FTIR-ATR spectrometer (Agilent Cary 630) equipped with a single-reflection diamond crystal at EcoPast laboratory (University of Santiago de Compostela). Measurements were recorded in absorption mode within the range of 4000 to 400 $cm^{-1}$ at a spectral resolution of 2 $cm^{-1}$ and accumulating 100 scans per sample. The background was obtained before analyzing each sample. Spectra were normalised by z-scores.

## 2.3. Sediment chronology

Samples of *P. oceanica* sheaths or *C. nodosa* debris were selected at 2-9 depths in each core for radiocarbon dating using $^{14}C$ accelerator mass spectrometry (DirectAMS laboratory; Table S2) following standard procedures (Karlén et al., 1968; Stuiver & Pollack, 1977). Samples were previously rinsed as in Belshe et al. (2019). The uppermost 30 cm of each core were dated by quantification of $^{210}Pb$ activities, through its daughter product $^{210}Po$, using alpha spectrometry with a PIPS detector (CANBERRA, Mod. PD-450.18 AM) at the Laboratori de Radioactivitat Ambiental (Universitat Autònoma de Barcelona). Supported $^{210}Pb$ was estimated as the average $^{210}Pb$ concentration of the deeper sediment layers analysed wherein $^{210}Pb$ activities reached constant values. Radiometric dates were calculated using the Constant Rate of Supply (CRS) dating model (Appleby & Oldfield, 1978). Both dating methods were combined to obtain age-depth models for the collected cores. The age-depth models were developed using the Bayesian modelling approach *Bacon* (Blaauw & Christen, 2011), run in the R statistical environment (version 3.6.0; R Core Team, 2019; Fig. S4). Radiocarbon dates were expressed as calibrated years before present (cal. yr BP). Dates were calibrated using the *marine 13* $^{14}C$ calibration curve (Reimer et al., 2013) and local corrections for the marine reservoir effect for the Andalusian coast ($\Delta R = 2 \pm 26$ years, Siani et al., 2000) and for Cabrera Island ($\Delta R = 24 \pm 26$ years, Riera Rullan, 2016).

## 2.4. Numerical procedures

Given the complex nature of the seagrass sediment matrix, the direct interpretation of FTIR spectroscopy is complicated because the spectral absorbance signatures are the result of many overlapped organic and inorganic compounds spectra (such as silicates, carbonates, cellulose, lignin, lipids, proteins…). To overcome this issue, the second derivative of the standardised absorbance sum spectrum was first calculated and used for wavenumber peak selection using the "andurinha" package (Álvarez Fernández & Martínez Cortizas, 2020). The strongest and most common diagnostic wavenumber peaks were selected and then analysed by principal component analyses (PCA), to explore the associations between them. The PCA enabled the correspondence between absorption peaks and specific compounds based on the fact that peaks with similar variability identified in the PCA are potentially indicative of a common precursor (Traoré et al., 2016, 2018). The assignment of correlated absorption peaks to specific inorganic and organic molecular structures was based on available literature (Table S3).

To facilitate the interpretation of the processes behind the principal components and assess their relationships with environmental drivers, local environmental and global climate variables were used together with FTIR absorption peaks in the PCA. Specifically, we included abiotic descriptors (XRF-measured elements such as Si, S, Br, Ca, Fe, Ti, Cl, K, Mn) as well as biotic variables related to total primary production (organic matter content, OM), seagrass production (seagrass COM), nutrient cycling and organic matter supply ($\delta^{13}C$ and $\delta^{15}N$). Global climate external factors included indices of Total Solar Irradiance (TSI, Vieira et al., 2011), Northern Hemisphere Temperature (NHT, Kobashi et al., 2013) and the North Atlantic Oscillation (NAO; Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012).

PCA analyses were calculated using the *pcaCoDa* command in the "robcompositions" package (Templ et al., 2011). This command allowed accounting for the compositional character of the log-ratios of XRF-elements intensities (Weltje & Tjallingii, 2008).

Generalised additive models (GAMs) were used to estimate temporal trends in the principal components scores. GAMs can model non-linear relationships between time and a response variable and can handle the irregular spacing typical in paleoecological time series (Simpson, 2018). Thin-plate regression splines were used to parametrise the smoothed functions of time (Wood, 2003). The automatic restricted maximum likelihood smoothness selection was used to select the optimal smoothness parameters (REML; Wood et al., 2016). We also checked for residual autocorrelation, and significant residual auto-correlation was not present for any of the time series.

The temporal stability of the principal components obtained was calculated using a common measure of stability, defined as the ratio of the mean ($\mu$) of the principal components scores to their standard deviation ($\sigma$) (Lehman & Tilman, 2000). The larger the value, the higher the temporal stability. To test for relationships between the temporal stability of the reconstructed ecological processes (i.e. identified principal components) and the mean level of that process (mean score value of the principal component), linear regressions were calculated. The strength of the relationship was assessed using the coefficient of determination ($R^2$). We considered the regression significant if the slope was significantly different from zero ($p < 0.05$).

All statistical analyses were conducted using R statistical software version 3.6.0 (R Core Team, 2019). Details of the materials and methods are provided in Supplementary Material.

# 3. RESULTS

## 3.1. Characteristic FTIR spectra of seagrass sediments

The FTIR sum absorbance spectrum of all the samples and its second derivative show the strongest absorbance for the bands in the region 400-1500 $cm^{-1}$. The strength of these absorption bands could be attributed to several inorganic and organic compounds which have multiple overlapped regions (Fig. 2). Such degree of overlapping makes the interpretation of FTIR spectra very complex and without the PCA, it would be almost impossible to explain the main differences between the FTIR spectra of the sediment samples.

Table S3 presents the band assignments of the selected peaks. Peaks from 400 to 1200 $cm^{-1}$ could be associated with the stretching vibration mode of the Si-O bond from silicates, including quartz and feldspar (Matteson & Herron, 1993; Margenot et al., 2017). Peaks around 1100 $cm^{-1}$, appearing together with peaks near 800 $cm^{-1}$, can be associated to the presence of biogenic silica (Meyer-Jacob et al., 2014; Sackett et al., 2015; Vogel et al., 2016). At the same region of Si-O bonds in minerals, vibrations could also be attributed to C-H out of plane bending and C-O stretching likely corresponding to aromatics and polysaccharides (Margoshes & Fassel, 1955; Giovanela et al., 2004; Wissel et al., 2008; Benito-González et al., 2019). The largest absorptions occur at ~1400 and 874 $cm^{-1}$. The co-occurrence of bands at 711, 855, 874, 1400-1500, ~1800, ~2500 $cm^{-1}$ can be associated to the vibration of carbonate ions (Tatzber et al., 2007; Bruckman & Wriessnig, 2013; Meyer-Jacob et al., 2014). Absorption bands along the region 1400-1500 $cm^{-1}$ could also correspond to diverse vibrations from multiple organic compounds, such as aliphatic chains, phenols, amides and aromatics (e.g. Giovanela et al., 2004; Gorgulu et al., 2007; Enev et al., 2014; Plis et al., 2014). Other bands that could also be linked to pure carbonates are ~2900 and ~3000 cm$^{-1}$, although they are even less characteristic because of their overlapping with the $CH_2$ stretching vibration of aliphatic components (Bruckman & Wriessnig, 2013; Plis et al., 2014). Peaks from 3400 to 3700 cm$^{-1}$ could be linked to O-H stretching and bending vibration, indicating the presence of clay minerals (Margenot et al., 2017). However, this region also overlaps with organic compounds, specifically to O-H and N-H stretching vibration modes from polysaccharides and proteins (Wissel et al., 2008). The only organic compounds that do not overlap with any minerogenic components are mainly proteins and also phenols, vibrating at 1653 and 1688 cm$^{-1}$, due to the vibration modes of C=O stretching and NH bending. These bands have been observed in seagrass tissues using FTIR (Rengasamy et al., 2011; Plis et al., 2014; Benito-González et al., 2019). Several peaks between 2920 and 2980 ($CH_2$ stretching vibration of aliphatic components; e.g. Wissel et al., 2008; Plis et al., 2014) do not overlap either with inorganic compounds.

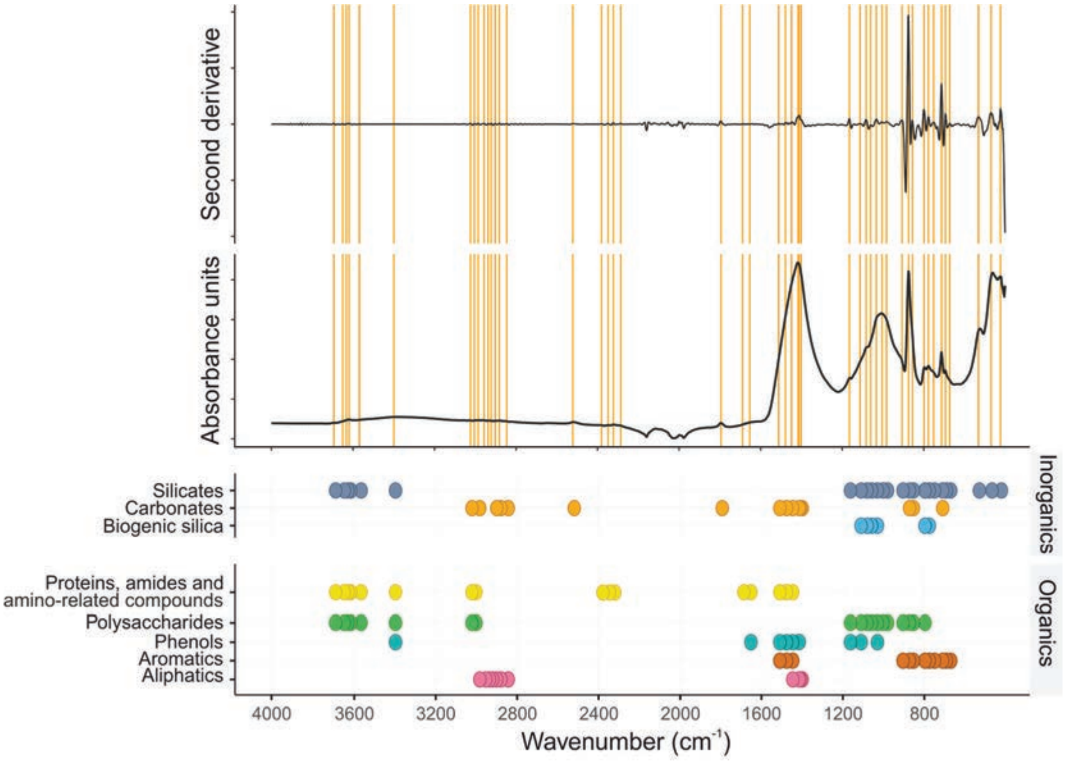

**Figure 2.** Second derivative sum spectrum and FTIR absorbance sum spectrum of seagrass sediments. Vertical yellow lines indicate the peaks selected mainly based on the second derivative sum spectrum. Coloured circles below indicate the bands assignments for main components determination.

## 3.2. Principal Component Analyses

### Coast of Andalusia

The three components extracted by $PCA_{AND}$, accounted for 84% of the total variance, of which $PC1_{AND}$, $PC2_{AND}$, and $PC3_{AND}$ explained a 70%, 9% and 5%, respectively (Fig. 3). The assignment of FTIR-ATR wavenumbers to specific compounds was based on available literature and can be found in Table S3.

The first principal component ($PC1_{AND}$) is characterised by moderate-to-high positive loadings corresponding to silicates, including clay minerals (Si, Ti, Fe, and absorbances at 423, 469, 672, 693, 751, 798, 906, 3399 to 3700 $cm^{-1}$ wavenumbers), and to diverse organic compounds, mainly aliphatics, such as lipids, nitrogen-containing compounds (aminoacids/proteins), and polysaccharides (1653, 1688, 1794, 2280-2521, 2840-3000, 3399 and 3570-3700 $cm^{-1}$), likely in the form of organo-clay complexes. On the other hand, $PC1_{AND}$ has moderate-to-high negative loadings linked to carbonates (Ca, 711, 855, 874, and 1401 to 1511 $cm^{-1}$) but also to lignin-like organic structures including polysaccharides, phenols, and aromatic hydrocarbons (S, OM, 1032-1164, 1448-1511 $cm^{-1}$; Fig. 3 and Table 2). $PC2_{AND}$ showed moderate-to-high positive loadings corresponding to polysaccharides (OM, seagrass COM, S, 1032-1164 $cm^{-1}$) and most likely to biogenic silica (Si, Mn, 777, 798, 1032-1112 $cm^{-1}$). $PC2_{AND}$ had negative loadings at absorbances mostly associated with carbonates (Ca, 711, 855, 874, 1401-1511, 1794 $cm^{-1}$), but also with silicates (Ti, K, Fe, 531 $cm^{-1}$), TSI, and NHT $cm^{-1}$ (Fig. 3 and Table 2). $PC3_{AND}$ showed positive loadings corresponding again to silicates (Ca, Si, K, 469, 531, 693, 751, 777, 798, 982-1082 $cm^{-1}$) and to climatic variables (NHT, TSI, NAO). $PC3_{AND}$ negative loadings are indicative of a mix of organic matter compounds, more specifically, aromatics, polysaccharides, proteins, and lipids, likely deriving from seagrass tissue (OM, seagrass COM, 711, 874, 1401, 1794, 1653, 2521 $cm^{-1}$). Iron, Mn, and S showed negative loadings as well in $PC3_{AND}$ (Fig. 3 and Table 2).

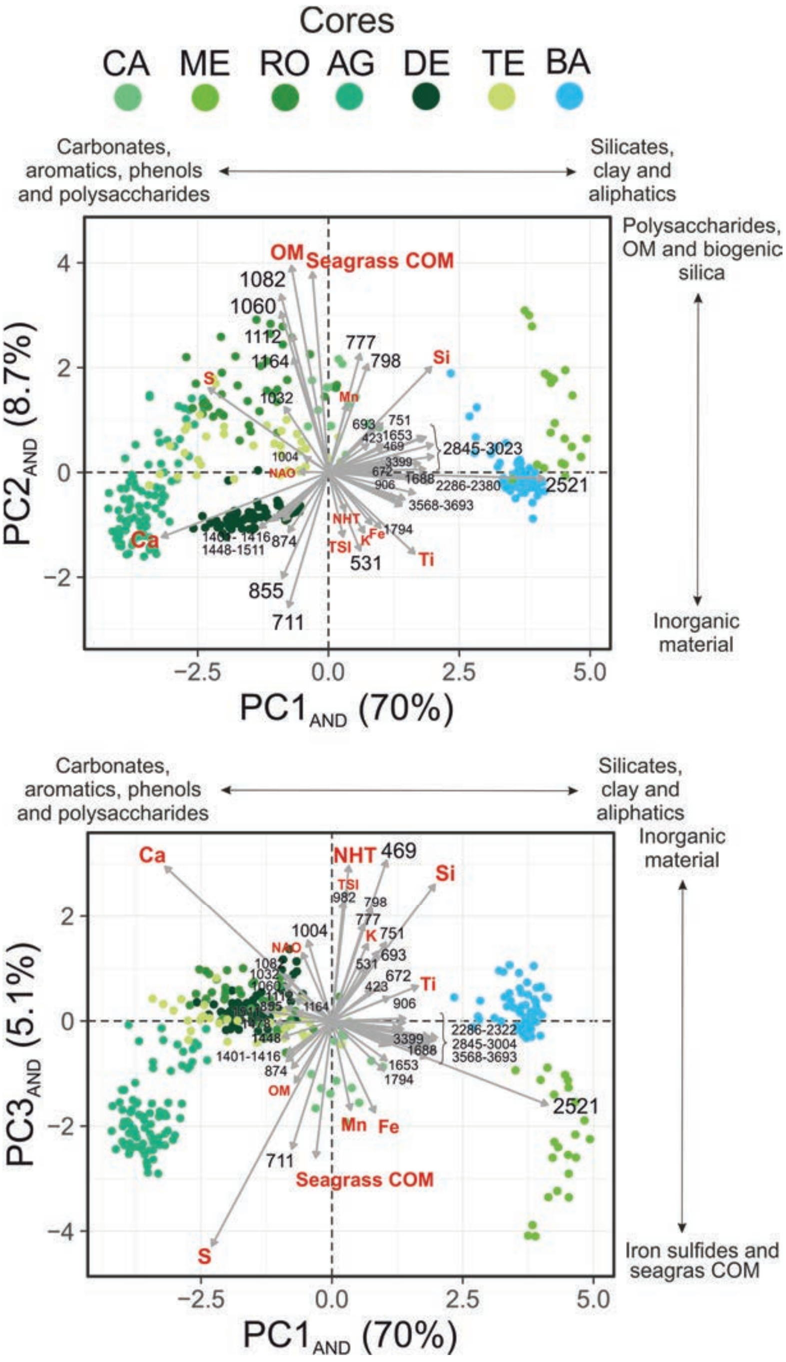

**Figure 3.** Biplots for the FTIR peaks together with explicative variables from the cores along the Andalusian coast ($PCA_{AND}$): content of organic matter (OM), content of coarse organic matter from the seagrass (Seagrass COM), XRF-measured elements (Al, Fe, Si, Ti, K, Mn, Ca, Cl, S), Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009) and Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013).

### Cabrera Island

The two components extracted by $PCA_{CAB}$, accounted for 77% of the total variance, of which $PC1_{CAB}$ accounted for 65% and $PC2_{CAB}$ for 12% (Fig. 4). The first principal component ($PC1_{CAB}$) is characterised by high positive loadings linked to aliphatics, such as lipids, and proteins but also polysaccharides (1794, 2286-3023, 3568-3700 cm$^{-1}$). $PC1_{CAB}$ showed negative loadings that could correspond to both silicates and aromatics and polysaccharides (OM, $\delta^{15}N$, Br, Cl, Fe, K, Ti, 423, 469, 531, 672, 693, 751, 777, 798, 906, 982 cm$^{-1}$ and several absorbances from 1004 to 1112 cm$^{-1}$; Fig. 4 and Table 2). $PC2_{CAB}$ showed positive loadings for variables related with carbonates and silicates (711, 798, 855, 906, 982, 1511 cm$^{-1}$, as well as, Fe, Si, Ti and Ca) while negative loadings would correspond to organic compounds, mainly proteins, carbohydrates, phenols, and lipids (OM, Br, Cl, S, $\delta^{15}N$, 1401-1416, 1653, 1688, 2845-3399 cm$^{-1}$), and to climate variables (NHT and TSI; Fig. 4 and Table 2).

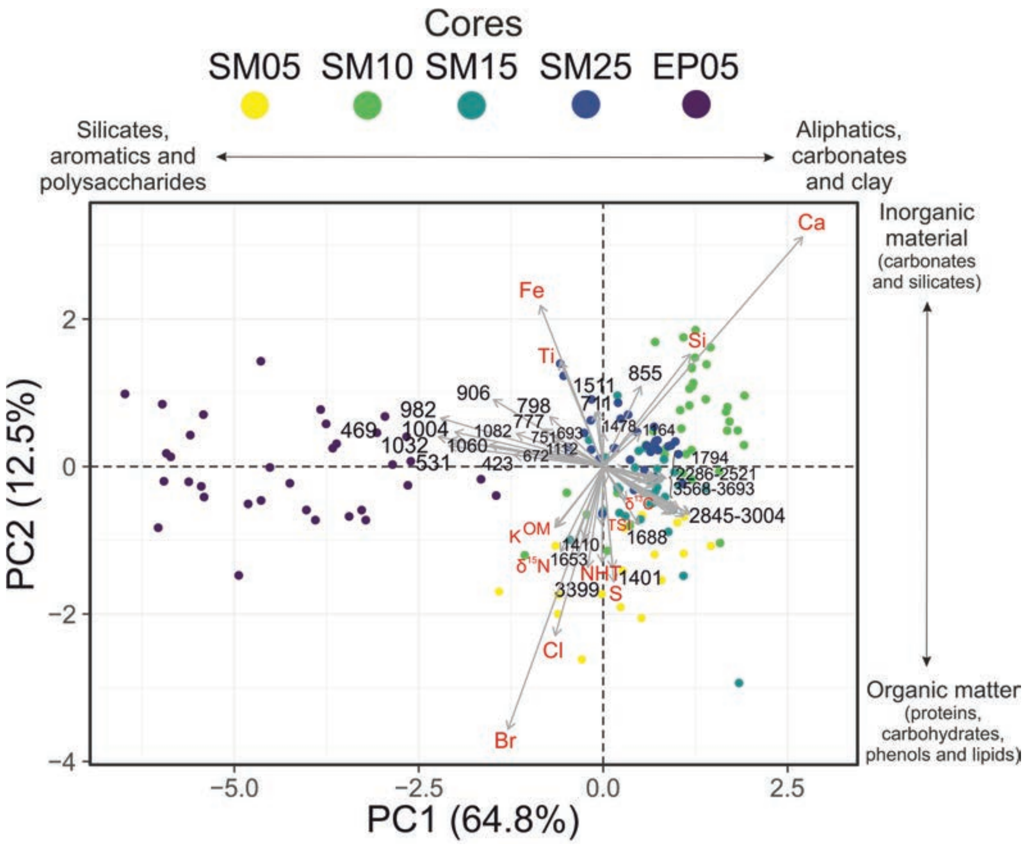

**Figure 4.** Biplot for the FTIR peaks together with explicative variables from the cores retrieved in Cabrera Island ($PCA_{CAB}$): content of organic matter (OM), carbon and nitrogen stable isotopes, XRF-measured elements (Al, Fe, Si, Ti, K, Cl, Ca and Br), Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009) and Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013).

**Table 2.** Factor loadings of the FTIR absorbances and rest of proxies used in PCA. Numbers in bold indicate peaks with the highest factor loadings. Numbers in bold and italic indicate peaks with moderate factor loadings. OM: organic matter content; Seagrass COM: organic material from seagrass (>2mm); TSI: Total Solar Irradiance (Vieira et al., 2011); NAO: North Atlantic Oscillation (a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009); NHT: Northern Hemisphere Temperature (Kobashi et al., 2013).

| | **ANDALUSIA** | | | **CABRERA** | |
|---|---|---|---|---|---|
| | **PC1** | **PC2** | **PC3** | **PC1** | **PC2** |
| | 70% | 8.7% | 5.1% | 64.8% | 12.5% |
| **423** | ***0.07*** | 0.05 | 0.05 | **-0.15** | 0.02 |
| **469** | **0.1** | 0.04 | **0.29** | **-0.28** | 0.05 |
| **531** | 0.06 | **-0.14** | **0.1** | **-0.26** | 0.04 |
| **672** | ***0.09*** | 0 | 0.06 | **-0.09** | 0.02 |
| **693** | ***0.08*** | ***0.08*** | **0.12** | **-0.09** | 0.05 |
| **711** | ***-0.07*** | **-0.24** | **-0.23** | -0.01 | **0.1** |
| **751** | **0.1** | ***0.09*** | **0.14** | ***-0.08*** | 0.04 |
| **777** | 0.06 | **0.21** | **0.17** | **-0.1** | 0.06 |
| **798** | ***0.07*** | **0.19** | **0.2** | **-0.09** | ***0.09*** |
| **855** | ***-0.08*** | **-0.19** | 0.02 | 0.06 | **0.14** |
| **874** | ***-0.07*** | **-0.11** | ***-0.08*** | 0.04 | -0.01 |
| **906** | **0.1** | -0.01 | 0.04 | **-0.19** | **0.11** |
| **982** | 0.02 | 0.01 | **0.21** | **-0.28** | ***0.08*** |
| **1004** | -0.04 | 0.03 | **0.14** | **-0.25** | 0.06 |
| **1032** | ***-0.08*** | **0.12** | 0.07 | **-0.26** | 0.05 |
| **1060** | ***-0.08*** | **0.28** | 0.06 | **-0.19** | 0.04 |
| **1082** | ***-0.08*** | **0.32** | 0.08 | **-0.15** | 0.06 |
| **1112** | -0.06 | **0.24** | 0.04 | ***-0.08*** | 0.03 |
| **1164** | -0.06 | **0.2** | 0.02 | 0.06 | 0.06 |
| **1401** | ***-0.08*** | ***-0.08*** | ***-0.07*** | 0.02 | **-0.17** |
| **1410** | ***-0.08*** | ***-0.08*** | -0.06 | -0.03 | **-0.14** |
| **1416** | ***-0.08*** | ***-0.08*** | -0.06 | -0.03 | **-0.12** |
| **1448** | ***-0.09*** | ***-0.08*** | -0.03 | 0.01 | -0.01 |
| **1478** | **-0.1** | ***-0.09*** | 0 | 0 | 0.06 |
| **1511** | **-0.12** | **-0.1** | 0.02 | -0.01 | **0.09** |
| **1653** | **0.1** | 0.05 | ***-0.07*** | -0.05 | **-0.14** |
| **1688** | **0.15** | -0.01 | -0.05 | 0.06 | **-0.1** |
| **1794** | **0.09** | **-0.1** | **-0.09** | **0.11** | -0.02 |
| **2286** | **0.18** | -0.02 | -0.03 | **0.09** | -0.02 |
| **2322** | **0.18** | -0.01 | -0.03 | **0.09** | -0.02 |
| **2348** | **0.17** | -0.01 | -0.03 | **0.09** | -0.03 |
| **2380** | **0.17** | -0.01 | -0.03 | **0.09** | -0.03 |
| **2521** | **0.38** | -0.01 | **-0.15** | **0.1** | -0.03 |
| **2845** | **0.18** | 0.05 | -0.05 | **0.15** | ***-0.08*** |
| **2881** | **0.17** | 0.06 | -0.06 | **0.15** | ***-0.08*** |
| **2902** | **0.17** | 0.06 | -0.04 | **0.14** | ***-0.09*** |
| **2922** | **0.1** | 0.02 | -0.04 | **0.12** | ***-0.08*** |
| **2937** | **0.11** | 0.02 | -0.03 | **0.12** | ***-0.08*** |
| **2955** | **0.16** | 0.02 | -0.05 | **0.13** | ***-0.07*** |
| **2985** | **0.17** | 0.01 | -0.05 | **0.13** | ***-0.07*** |
| **3004** | **0.19** | 0.03 | -0.03 | **0.12** | ***-0.07*** |
| **3023** | **0.13** | 0.03 | -0.01 | **0.12** | ***-0.08*** |
| **3399** | **0.1** | 0.01 | -0.04 | -0.03 | **-0.17** |
| **3568** | **0.14** | -0.05 | -0.04 | ***0.07*** | -0.05 |
| **3619** | **0.13** | -0.06 | 0 | ***0.07*** | -0.02 |
| **3632** | **0.13** | -0.05 | 0 | ***0.07*** | -0.02 |
| **3650** | **0.12** | -0.05 | -0.01 | **0.09** | -0.02 |
| **3693** | **0.15** | -0.04 | -0.03 | **0.1** | -0.02 |
| **Si** | **0.18** | **0.19** | **0.24** | **0.15** | **0.19** |
| **S** | **-0.21** | **0.15** | **-0.4** | 0.02 | **-0.2** |
| **Br** | - | - | - | **-0.16** | **-0.45** |
| **Cl** | - | - | - | ***-0.08*** | **-0.29** |
| **K** | 0.06 | **-0.11** | **0.14** | ***-0.08*** | **-0.1** |
| **Ca** | **-0.3** | **-0.11** | **0.27** | **0.34** | **0.39** |
| **Ti** | **0.15** | **-0.14** | 0.06 | ***-0.07*** | **0.18** |
| **Mn** | 0.03 | **0.12** | **-0.16** | - | - |
| **Fe** | ***0.08*** | **-0.09** | **-0.16** | **-0.11** | **0.28** |
| **OM** | ***-0.07*** | **0.37** | **-0.11** | ***-0.08*** | **-0.1** |
| **Seagrass COM** | -0.03 | **0.35** | **-0.24** | - | - |
| **$\delta^{13}$C** | - | - | - | 0.04 | -0.06 |
| **$\delta^{15}$N** | - | - | - | ***-0.07*** | **-0.15** |
| **TSI** | 0.03 | **-0.11** | **0.23** | 0 | **-0.1** |
| **NAO** | -0.05 | 0 | **0.12** | 0 | -0.03 |
| **NHT** | 0.03 | ***-0.07*** | **0.28** | 0 | **-0.16** |

### Spatial patterns of PC scores

The box-plot of the component scores of $PCA_{AND}$ (Fig. 5A) showed some clear differences among cores. Cores located in the Mediterranean Andalusian side (AG, TE, DE) had lower scores in $PC1_{AND}$ than those situated at the Alboran Sea (ME, CA, BA), except for RO, one of the two stations situated near the Mediterranean-Alboran Sea limit. There is also a spatial gradient for $PC2_{AND}$ scores, although not as clear as in $PC1_{AND}$, with cores located to the east (DE, AG, BA, TE) showing lower scores. ME and AG had the highest scores for $PC3_{AND}$ while CA had medium values and RO, DE, BA, and TE had the lowest.

The box-plot of the $PCA_{CAB}$ scores (Fig. 5B) showed a clear difference between bays for $PC1_{CAB}$, with EP05 having lower scores than SM cores. SM10 had the highest PC1 scores, higher than the rest of the cores from the same bay. As for $PC2_{CAB}$ scores, SM05 had lower scores than the rest, while SM10 and SM25 had the highest mean values.

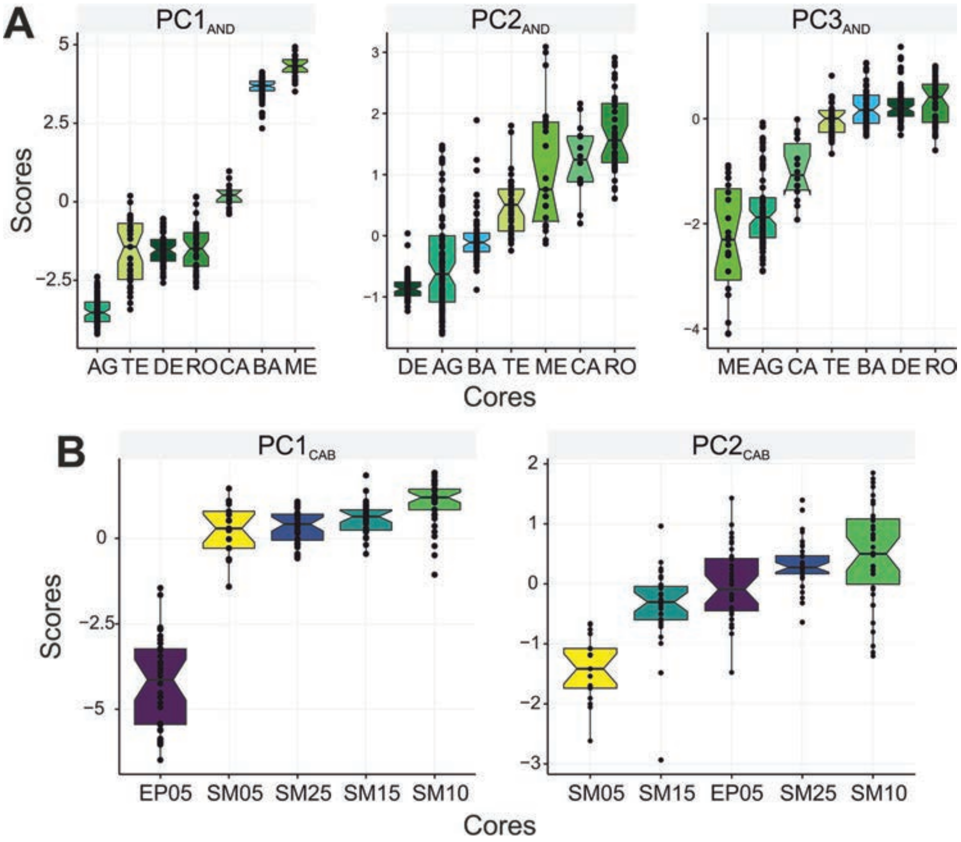

**Figure 5.** Boxplot of the principal components (PC) scores for every core along the Andalusian coast –AND– (A) and from the Cabrera Island –CAB– (B). Boxplots are sorted by median value from the lowest to the highest.

## Temporal trends of PC scores

For every principal component, we found strong and significant positive relationships between the long-term temporal stability and the mean score value of each core in both areas, Cabrera and Andalusia (Fig. 6A and 6B).

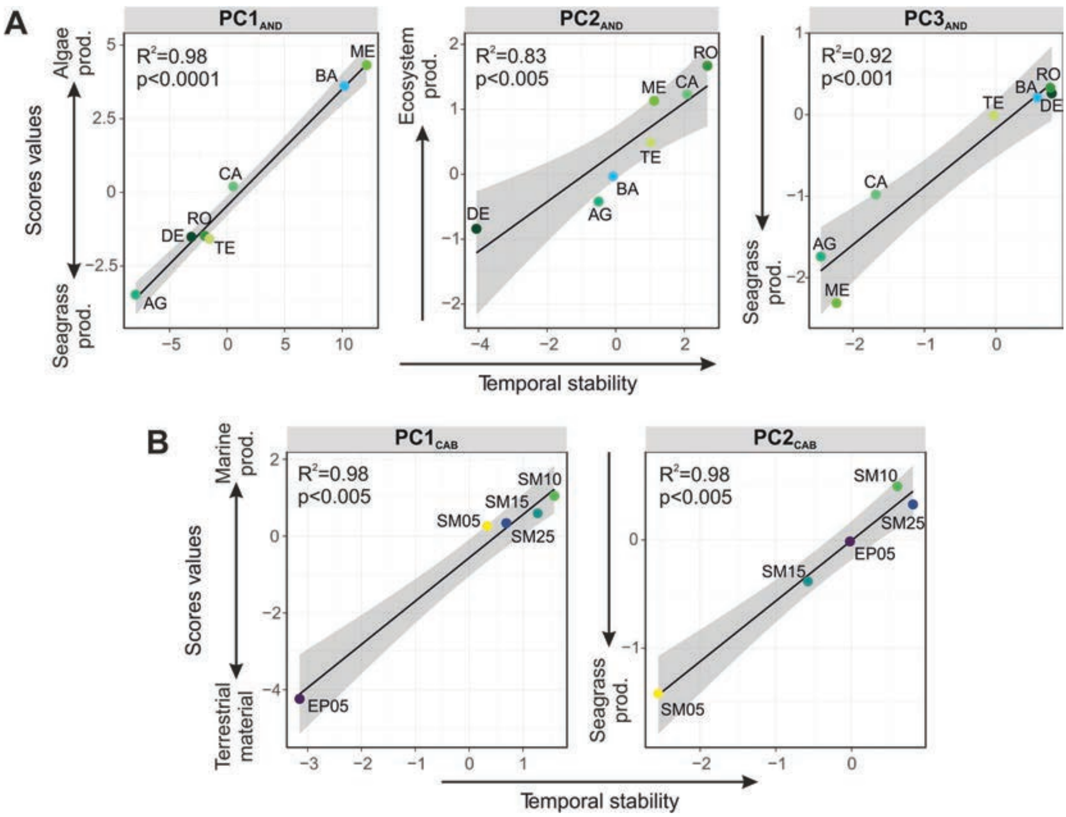

**Figure 6.** Relationships between principal components (PC) temporal stability and level of mean score value of that component for every core in Andalusia –AND– (A) and Cabrera Island –CAB– (B). Black lines indicate a regression line and grey areas are prediction intervals. Labels next to points indicate the code of the core.

Andalusia principal components scores showed no clear or common temporal trend among cores for PC1$_{AND}$ and PC2$_{AND}$ (Fig. 7A). PC2$_{AND}$ showed recent (over the last one or two centuries) temporal trends towards negative scores in CA, ME, and RO, while BA, AG and TE, showed recent temporal trends towards positive values. PC3$_{AND}$ showed recent temporal trends towards positive scores since ~100-50 cal. yr BP (AD ~1850-1900), trends more or less conspicuous, in every core. In cores reaching ages beyond 600 cal. yr BP (RO, AG, DE, TE), overall lower scores values of PC3$_{AND}$ were observed from ~150 to 650 cal. yr BP.

PCA$_{CAB}$ scores temporal trends were very variable. They did not show any clear common trend among cores for any of the principal components (Fig. 7B). SM10 had temporal trends towards negative score values for PC1$_{CAB}$ and PC2$_{CAB}$, especially for the last 400 years. Slighter temporal trends, also towards negative values, were observed at SM15 for PC1$_{CAB}$ and PC2$_{CAB}$ over the last 1800 years. SM05 and EP05 had noisier trends, although with an overall tendency also towards negative values for PC2$_{CAB}$ over the last centuries.

# 4. DISCUSSION

## 4.1. Terrestrial influence on marine production and OM preservation

PC1$_{AND}$ likely indicates the degree of aliphaticity (positive loadings) versus aromaticity (negative loadings) of the humic sediment material. This could be related to the composition of the main source materials (Rashid, 1985; Giovanela et al., 2004), with seagrass-derived OM corresponding to negative loadings and algae-derived OM associated to positive loadings. Moreover, the sedimentary environment prevailing at the time of deposition, which is closely linked to the living communities in the overlying water column, also influences the OM preservation (Schmidt et al., 2011) and hence the relative content of aliphatic and aromatic compounds.

In Andalusia, PC1$_{AND}$ positive loadings are indicative of meadows growing on terrigenous sediments with the accumulation of lipids, nitrogen-containing compounds and polysaccharides, highly aliphatic compounds abundant in marine algal-derived OM (Giovanela et al., 2004; Mecozzi et al., 2009; Villacorte et al., 2015). Seagrasses tissues have a low content of nitrogen (1–3%; Duarte, 1990), so they are less likely to significantly contribute to the sediment nitrogen compounds. Significant seagrass losses and higher algal growth (macro- and micro-), deriving in an increased accumulation of allochthonous carbon from algae and microbes in seagrass sediments, usually occur in meadows influenced by terrigenous runoff, due to increased water turbidity and nutrient concentrations (Ralph et al., 2006; Macreadie et al., 2012; Liu et al., 2016; Mazarrasa et al., 2017a). FTIR absorbances also indicated anaerobic sediment conditions, given the abundance of carbonyl groups ($C=O$ ~1670-1790 $cm^{-1}$), effectively preserved under low-oxygen sediments (Rashid, 1985a), and clay, likely from continental runoff discharges, reducing sediment porosity and oxygenation, and maintaining a low redox potential. Clay minerals can also form organo-clay complexes, retarding the degradation of organic matter (Baldock & Skjemstad, 2000). These sediment conditions would help in the accumulation of aliphatics and nitrogen-rich compounds, which are otherwise preferentially degraded in aquatic environments (Derenne & Largeau, 2001; Tremblay et al., 2011).

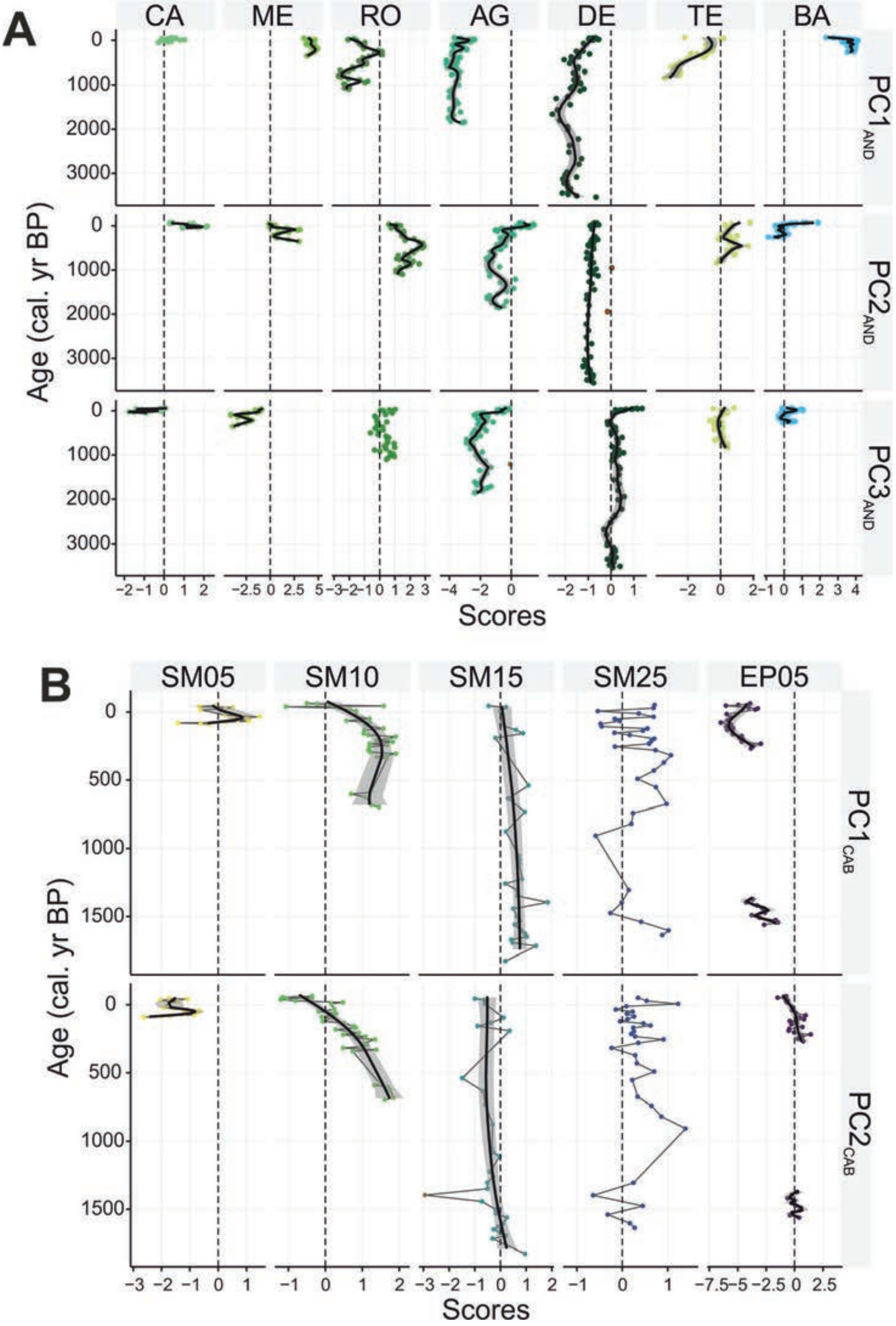

**Figure 7.** Depth records of the principal components (PC) scores obtained in PCA for every core along the coast of Andalusia –AND– (A) and from the Cabrera Island –CAB– (B). Abbreviations above records (CA, ME…) correspond to the code of the core. Black solid lines indicate the fitted smooth functions of time (GAM models, formula = $y \sim s(x)$) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant ($p < 0.05$) trends are shown. Red points were considered outliers and not included in GAM models.

On the other side, negative loadings correspond to meadows growing on carbonate sediments less influenced by terrestrial inputs and where *P. oceanica* is very likely the primary OM source, due to the abundance of its main structural compounds: aromatics, phenolics, lignins, and also polysaccharides (Kaal et al., 2016). Therefore, $PC1_{AND}$ scores along the cores could indicate relative changes of the two main primary producers in a seagrass meadow: algae and seagrass, as well as of sedimentary conditions, thus, taking into account that both factors are probably not independent from each other.

This interpretation is consistent with the almost perfect division of $PC1_{AND}$ scores between cores located at the Alboran (CA, ME, RO, BA) and Mediterranean seas (AG, DE, TE; Fig. 5A), given that Alboran waters are richer in nutrients and phytoplankton than Mediterranean waters (Muñoz et al., 2015; del Carmen García-Martínez et al., 2019). A similar component to $PC1_{AND}$ is reconstructed in the Cabrera Island, although the organic compounds involved under similar environments are not the same, reflecting clear differences between study areas. $PC1_{CAB}$ would be related to a gradient between marine production, higher in Santa Maria Bay (SM), and terrestrial inputs, higher in Es Port Bay (EP), a closed bay. A higher delivery of terrestrial material in EP is coherent with the occurrence of the main pluvial network discharges in EP (Rodríguez-Perea & Servera, 1993). Under moderate terrestrial inputs (EP), Cabrera meadows sediments showed a higher abundance of polysaccharides and aromatics, while in Andalusia, under higher terrestrial inputs, the main organic compounds were aliphatics, lipids and proteins. Higher OM degradation rates may explain the lower content of aliphatics under terrestrial influence in Cabrera sediments. Holmer et al. (2003) reported high anaerobic degradation rates in EP due to the combination of high OM accumulation and more carbonate content as compared to coastal mainland meadows. Hence, the more labile aliphatics would be further consumed in EP and sediments would get enriched in aromatics and polysaccharides terrestrial compounds, more difficult to degrade. The aliphatics predominance in SM points to an elevated phytoplanktonic input in the sediments of this bay. The sediment carbon isotope ratios also pointed to this, as they showed depleted values of $\delta^{13}C$ (-20.6 ± 1.7‰, Table S4), close to the signal characteristic of seston (e.g. ~ -22 ± 2 ‰, Papadimitriou et al., 2005). It seems that seagrass meadows in Cabrera have higher sestonic inputs than in Andalusian meadows, where sediment $\delta^{13}C$ is closer to that of seagrass material (-16 ± 2‰, Table S4), most likely because Cabrera meadows are located in bays with longer water residence times would favour seston sedimentation (4 -15 days in bays of Cabrera -Marbà et al., 2002; Orfila et al., 2005- while ~ <1 day in the open meadows of Andalusia). A higher phytoplanktonic contribution in Cabrera Island meadows compared to others Balearic meadows was already observed by Holmer et al. (2004).

## 4.2. Ecosystem and seagrass production

$PC2_{AND}$, $PC3_{AND}$ and $PC2_{CAB}$ could be all related to processes of marine community or seagrass production. Positive loadings of $PC2_{AND}$ are likely linked to the whole community production since they include total OM content, seagrass COM, biogenic silica and polysaccharides, ubiquitous and abundant compounds in marine photosynthetic organisms (Burdige, 2006). Manganese is typically associated with biogenic silica, as a surface coating (Ingall et al., 2013). Therefore, its positive loading quite close to the silica signal in $PC2_{AND}$ suggests a biogenic origin for both accumulations (Fig. 3). Polysaccharides can be preferentially degraded in marine sediments (Arnosti et al., 1994; Mckew et al., 2013), so its accumulation independent of the clay content is likely indicative of high primary production. Moreover, $PC2_{AND}$ scores along the cores did not show clear common degradation trends of polysaccharides with ageing (except maybe in AG and BA where the recent sediment layers have a higher content of polysaccharides, Fig. 7A).

Negative loadings of $PC3_{AND}$ are likely indicative of seagrass production, with a mix of organic compounds including aromatics, carbohydrates, phenols, proteins, and lipids that are found in *P. oceanica* tissues (Kaal et al., 2016). Seagrass production seems to be closely linked to sediment conditions that enhance iron-sulfides precipitation, given the high negative loadings for Fe, S, and Mn (Fig. 3 and Table 2). These sediment conditions seem to be favoured under certain climatic conditions that will be later discussed.

In coastal vegetated marine sediments, sulfate reduction is the main pathway of organic matter mineralisation due to the prevailing geochemical conditions (anaerobia, high availability of organic matter, and dissolved sulfates; Howarth, 1984). The observed coupling between sulfate reduction rates and the seagrass photosynthetic activity led to the hypothesis that plant root exudates, providing labile organic carbon, fuelled sulfate-reducing bacteria (Oenema, 1990; Nielsen et al., 2001; Otero et al., 2014). Sulfides have phytotoxic properties to seagrasses, negatively affecting their production and growth and increasing their mortality (Holmer & Hasler-Sheetal, 2014). These negative effects were observed in seagrasses growing in contrasting sediments (Holmer & Kendrick, 2013), although meadows in carbonate sediments show higher sensitivity to anoxia and sulfides due to low iron contents (Holmer et al., 2003; Ruiz-Halpern et al., 2008).

Besides the classic limitation of iron for growth (Bristow et al., 2017), iron can further limit seagrass production through sulfides buffering. Iron has a key role re-oxidising and burying a significant part of sulfides compounds as iron-sulfide, such as pyrite ($FeS_2$), which reduces plant exposure to sulfide and can stimulate seagrass growth rates (Chambers et al., 2001; Holmer et al., 2005; Marbà et al., 2007, 2008; Ruiz-Halpern et al., 2008; Devereux et al., 2011; Xu et al., 2019; Li et al., 2020). The presence of iron sulfides, mainly pyrite, has been observed in sediments of coastal vegetated ecosystems including seagrass meadows (Holmer et al., 2006; Ku et al., 2008; Ferreira, 2010). Pyrite formation in marine ecosystems is primarily limited by the amount and reactivity of OM inputs into the sediment but also by the abundance and reactivity of detrital iron minerals (Berner et al., 1985; Otero et al., 2014). Therefore, a higher input of iron (probably together with other nutrients) to seagrass meadows could ameliorate the adverse effects of sulfide stress and allow elevated seagrass production and OM burial. Higher seagrass production and OM burial would enhance sulfate reduction rates and, together with the higher iron availability, pyrite formation would also increase, explaining the positive correlation between seagrass COM, Fe and S found in this study. The high loading of Mn together with Fe and S could be a result of coprecipitation of Mn (II) with iron sulfides in anoxic-sulfidic environments (e.g. Otero & Macias, 2003).

In Cabrera, $PC2_{CAB}$ is most likely indicating changes in the seagrass production. Most of the FTIR absorbances loading in this component are associated with seagrass compounds (carbohydrates, phenols, lipids), which also appear in $PC3_{AND}$, its equivalent component in the coastal mainland cores. The core with the most negative scores for $PC2_{CAB}$ is SM05, which had the highest amount of seagrass detritus, as observed during laboratory processing - reinforcing the $PC2_{CAB}$ interpretation. A difference between the seagrass production between Cabrera and Andalusia, as reconstructed here, is the fact that seagrass production in Cabrera is not related to iron. This was not expected given the low content of iron in carbonate sediments. However, our results are consistent with previous research in the area showing that iron additions did not stimulate seagrass growth in SM and did not completely eliminate nutrient limitation in neither of two the bays studied here (Holmer et al., 2005). This fact, together with the positive loading found for $\delta^{15}N$ in the seagrass production component ($PC2_{CAB}$), suggests that nitrogen could be the main limiting nutrient in meadows around the Cabrera Island.

The highly significant correlation between current mean seagrass shoot densities and their most recent $PC3_{AND}$ and $PC2_{CAB}$ scores values (approximately from 2000 to 2018; Fig. S6), reinforces our interpretation of negative scores from both principal components being related with seagrass production. Mean seagrass shoot densities for each study site were calculated from collected literature data covering diverse periods between 2004 and 2018 for Andalusia and between 2000 and 2007 for Cabrera (Table S5). All reconstructed ecosystem and seagrass production processes are negatively correlated to inorganic terrigenous elements. This does not necessarily indicate higher terrestrial runoff. Instead, it is more likely related to a dilution effect in which less seagrass production implies less OM and higher inorganic material content.

### 4.3. Climate influence on long-term nutrient availability and seagrass production

Seagrass production in Andalusia was correlated with higher sediment concentration of iron sulfides and anticorrelated with global climate variables ($PC3_{AND}$ in Fig. 3), indicating that seagrass production is enhanced during periods of lower solar irradiance and air temperature and negative NAO phases. Present and past climate in southern Iberia is related to the NAO index, mainly regarding changes in precipitation, with negative NAO phases coinciding with wetter periods and enhanced fluvial discharges (Trigo et al., 2004; Liquete et al., 2005; Nieto-Moreno, 2012; Benito et al., 2015; Sánchez-López et al., 2016). These terrestrial discharges would supply nutrients, including iron, which would buffer sulfides and seagrass production would ultimately increase. Ausin et al. (2014) reported a positive correlation between periods of increased paleoproductivity and negative NAO phases in the Alboran Sea. They hypothesised that during negative NAO phases, atmospheric conditions derived in increased seawater vertical mixing and intensified upwelling conditions. Prevalent upwelling conditions during negative NAO phases would also supply nutrients and iron into the coastal area.

Global climate variables - air temperature and, to a lesser extent, solar irradiance - are also correlated with seagrass production in Cabrera ($PC2_{CAB}$ in Fig. 4). This relationship could also be linked to changes in local/regional climate, and hence, in terrestrial inputs, which could cause changes in nutrient availability. However, unravelling the exact mechanism is currently a complex endeavour because local climate reconstructions did not find correlations with global climate variables around the Balearic Islands (Cisneros et al., 2015).

### 4.4. Spatial patterns and temporal stability

Along the mainland coast, the main source of OM was found to be algal in two *P. oceanica* meadows (CA, ME) and in the only *C. nodosa* meadow (BA) of this study (Fig. 5A). In these meadows, the OM source has barely changed within the last centuries (Fig. 6A). A higher contribution of algal vs seagrass material in CA and ME is consistent with their location in the western side of the Andalusian coast, receiving higher river water discharges due to their wetter climate and being closer to areas subjected to periodic upwelling of deeper waters with high nutrient concentrations (Sarhan et al., 2000; Liquete et al., 2005; Macías et al., 2007; CAGPDS, 2014). BA is a meadow located under the influence of a Mediterranean river with the highest capacity in Andalusia (Andarax, transporting more sediment per water discharge, Liquete et al., 2005), and with a strong torrential character. This area is therefore subjected to sudden and high sediment discharges, very unstable environmental conditions under which *P. oceanica* cannot survive, and it is hence replaced by *C. nodosa*. *C. nodosa* is an opportunistic species with a higher capacity of recovery and to acclimate to environmental variability (e.g. Marbà et al., 1996a; Cancemi et al., 2002; Olesen et al., 2002; Kilminster et al., 2015). On the other hand, meadows with higher seagrass than algal production are those located more to the east (AG, DE, and TE; Fig. 5A), areas where the climate is more arid and water river discharges are much lower and irregular (Fernández Salas et al., 2015). The irregular terrestrial influence may explain the higher variability regarding changes in primary producers (Fig. 6A). The only exception to this geographical pattern was RO, situated a few miles westward from BA, but still near to the Alboran-Mediterranean limit, in a very shallow (1 m) *P. oceanica* barrier-reef.

In general, the higher the meadow ecosystem production ($PC2_{AND}$), the more to the west the meadow is located. An environmental gradient along the coast most likely related to the water nutrient availability gradient (with richer waters towards the west), which seems the main driver behind the ecosystem production. Moreover, ecosystem production showed more temporally stable dynamics in meadows with higher production, most probably because of more stable environmental conditions with less torrential terrestrial influence ($PC2_{AND}$ vs temporal stability in Fig. 6A). On the other hand, seagrass production level showed a negative relationship with its temporal stability, both in Andalusia and in Cabrera (Fig. 6A and B), which reveals a long-term trade-off between the stability and level of seagrass production. Similar trade-offs were also observed in temperate forest ecosystems (Albrich et al., 2018), as well as in agricultural systems (Deguines et al., 2014; Montoya et al., 2019). Meadows with lower stability may also have lower long-term resilience. The temporal dynamics of ecosystems with low resilience that approach a critical transition, show an increase in variance (Scheffer et al., 2015). Therefore, meadows with higher long-term stability in seagrass production, are likely to have higher resilience and resistance, being also easier for managers to maintain.

In the Cabrera Island, EP showed higher terrestrial inputs and lower marine production compared to SM ($PC1_{CAB,}$ Fig. 5B), which is consistent with the higher discharge of the main pluvial network in EP (Rodríguez-Perea & Servera, 1993). Mazarrasa et al. (2017a) also reported a higher contribution of allochthonous carbon in EP compared to SM. Regarding the seagrass production in the island ($PC2_{CAB}$), SM05 stands out as the station with the highest seagrass production with deeper stations having lower production (except for SM10) (Fig. 5B). Lower seagrass production with water depth is a gradient widely described, related to reduced seagrass growth and production at physiological but mostly at structural levels (Dennison, 1987; Olesen et al., 2002; Collier et al., 2007; Enríquez et al., 2019).

## 4.5. *C. nodosa* compared to *P. oceanica* long-term dynamics

As for the long-term dynamics of the production of the *C. nodosa* meadow in this study (BA), our results point to a meadow that does not seem much different from some *P. oceanica* meadows. Seagrasses with smaller sizes tend to be less productive and have lower biomass (Duarte & Chiscano, 1999; O'Brien et al., 2018a). However, the median score values of the reconstructed processes $PC2_{AND}$ and $PC3_{AND}$ for BA are within the range of other *P. oceanica* meadows (Fig. 5A). There are, therefore, some *P. oceanica* meadows showing lower levels of long-term production than *C. nodosa*. This means that the long-term community and seagrass production of this *C. nodosa* meadow are not the lowest as it was expected. In a compilation by Duarte & Chiscano (1999), *C. nodosa* showed almost 2-fold lower values of above and belowground production (1.3 and 0.2 g DW $m^{-2}$ $day^{-1}$, respectively) compared to *P. oceanica* (2.4 and 0.2 g DW $m^{-2}$ $day^{-1}$, respectively). However, other studies have reported higher values of leaf production for *C. nodosa* that are comparable to other seagrass species such as *P. oceanica* (Rismondo et al., 1997; Agostini et al., 2003; Cunha & Duarte, 2007; Terrados et al., 2006 and references therein; Sghaier et al., 2011). In our study, the main difference between the *C. nodosa* meadow and most of the *P. oceanica* meadows is related to the relative production of algae versus seagrass ($PC1_{AND}$ in Fig. 5A). The *C. nodosa* meadow shows a higher algal production relative to the seagrass compared to most of the *P. oceanica* meadows. This is in agreement with studies showing that the associated community of *C. nodosa* showed higher biomass of algal epiphytes compared to *P. oceanica* (Mazzella et al., 1998; Mabrouk et al., 2014b). Another difference of the *C. nodosa* meadow is that it is the only seagrass meadow showing a clear tendency of recovery of its production since AD ~1950 after the overall seagrass decline along the Andalusian coast since AD ~1850 (Fig. 7A). This is likely indicative of the greater capacity of recovery of the *Cymodocea* genus compared to *Posidonia* spp. (O'Brien et al., 2018a). However, the comparison between the two seagrass species is not balanced in our study, because we only investigated one core from a *C. nodosa* meadow so the results should not be extrapolated. Further studies aiming to elucidate the similarities and differences between the long-term dynamics of the seagrass species, should include more cores from meadows dominated by smaller species.

## 4.6. Temporal trends

In general, $PC1_{AND}$, $PC2_{AND}$ and $PC1_{CAB}$ scores did not show common temporal trends throughout time (Fig. 7), which points to local factors as the main drivers of changes in primary producers and ecosystem production. However, the GAMs did show a clear common trend for $PC3_{AND}$, component related to seagrass production in Andalusia (Fig. 7A). More specifically, a decrease in seagrass production is observed in Andalusia since AD ~1850/1900, in line with the general seagrass decline trend since AD 1850, observed by Marbà et al. (2014). In cores reaching ages beyond 600 cal. yr BP (RO, AG, DE, TE), lower scores values of $PC3_{AND}$ (indicating higher seagrass production) were observed during the Little Ice Age (LIA; ~150 to 650 cal yr BP). Considering the anticorrelation between global climate variables and seagrass production ($PC3_{AND}$; Fig. 3 and Table 1), the long-term variability of seagrass production is most likely related to changes in global climate, although combined negative impacts of both local anthropogenic changes and global climate cannot be discarded, especially during the decrease of the last century.

Sea surface water temperatures (SST) in the Alboran Sea have been rising coeval with global warming, with a sharp and unprecedented SST increase since 150 cal. yr BP (AD ~1850, Fig. 8; Nieto-Moreno, 2012). Temperature rise can directly affect the performance of seagrasses, since they show high sensitivity to seawater warming, at physiological and population levels, decreasing their growth and even causing plant mortality (Mayot et al., 2005; Díaz-Almela et al., 2009; Marbà & Duarte, 2010; Collier & Waycott, 2014; Hendriks et al., 2017). The biogeochemical process closely related to long-term seagrass production according to our results in Andalusian seagrass meadows, sulfate reduction, is also enhanced by increased water temperature (Koch et al., 2007; Sanz-Lázaro et al., 2011). Since AD ~1950 there is also a trend towards more positive values of the NAO index and, as mentioned above, positive NAO phases in the Alboran Sea are linked with lower terrestrial discharges and upwelling events, limiting nutrient and iron availability to the seagrass meadows (Ausin et al., 2014; Sánchez-López et al., 2016). Therefore, the sediment buffering capacity of sulfides would be most likely surpassed during drier and warmer periods due to a higher accumulation of the phytotoxic sulfides and lower arrival iron inputs, further compromising the seagrass development. The LIA is evidenced as a colder and wetter period with higher riverine influence due to lower solar irradiance and lower NAO values (Nieto-Moreno, 2012; Oliva et al., 2018). A higher delivery of terrestrial material together with a higher frequency of upwelling events would have brought nutrients and iron into the coastal area stimulating seagrass production and explaining the negative $PC3_{AND}$ score values reached during the LIA (Fig. 8).

Previous studies showed that most of our study sites are currently experiencing interannual-decadal negative growth rates (CAGPDS, 2018). Our results indicate that this trend is likely to have already started around AD ~1850 along the mainland coast, moment when the sea also started to warm up, what would point to temperature as a key factor that affected seagrasses performance (Fig. 8). In contrast, long-term negative trends of seagrass production during the last centuries were not evident in our cores from Cabrera Island ($PC2_{CAB}$, Fig. 7B). However, recent studies have also shown

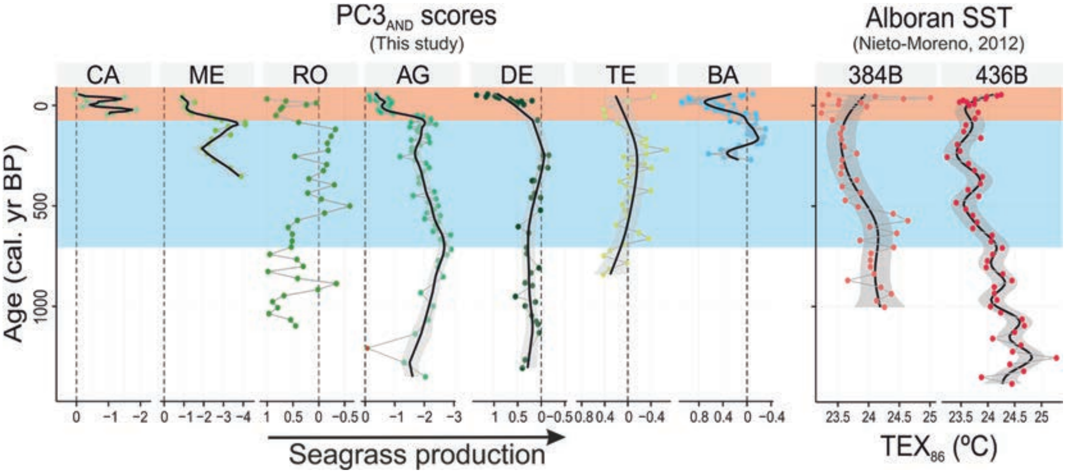

**Figure 8.** Depth records of PC3AND scores obtained in PCAAND plotted together with Alboran sea surface temperature (SST) reconstructions (Nieto-Moreno, 2012). Abbreviations above records (CA, ME…) correspond to the code of the core. SST were based on archaeal isoprenoid tetraether membrane lipids, the $\mathrm{TEX}_{86}$ index (Schouten et al., 2002). Light red area highlights the recent warming period observed in Alboran SST records and the light blue area indicates the Little Ice Age period. Positive scores of PC3AND are related to lower levels of seagrass production. Black solid lines indicate the fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant ($p < 0.05$) trends are shown

current negative seagrass growth rates in this specific island of the Balearics, where seawater temperature rise was found to be the main driver (Marbà et al., 2005; Marbà & Duarte, 2010). This poses the question of why Cabrera meadows were not registering a long-term negative effect derived from global and seawater warming. It turns out that an SST reconstruction around the Balearic Islands did not show the centennial warming trend registered in the Alboran Sea since the industrialisation, although this could be a consequence of a much lower temporal resolution in the study of Cisneros et al. (2015). The western Alboran anticyclonic gyre showed a more intensive warming trend than Balearic waters in summer and autumn over the 1982–2012 period (Shaltout & Omstedt, 2014). We should also consider the role of negative anthropogenic effects along the coast of Andalusia where the population has been growing since ~1920 (Instituto de Estadística de Andalucía, 1999), while in Cabrera Island there has never been a permanent population of more than ~50 people (Frontera et al., 1993). In fact, the steepest decline reaching the lowest values of seagrass production is observed at DE, a meadow impacted by industrial discharges over the last decades (Moreno et al., 2001, 1999). The combined negative impacts of local anthropogenic changes and a plausible more acute seawater warming in the Alboran sea, could explain why declining trends started earlier in seagrass meadows along the coast of Andalusia. The fact that Andalusian meadows are close to the *P. oceanica* geographical range limit (Mateo Ramírez et al., 2016) likely made them more vulnerable and could have also played a role in their worse past and present state. Besides, these results also highlight the role of past conditions in driving the present dynamics of seagrass ecosystems. This legacy should be considered when trying to understand the current worse state of the Andalusian meadows, with lower population growth rates than in the Balearic Islands (Marbà et al., 2005). The influence of past disturbances has also been found to be a factor driving the contemporary dynamics of terrestrial forests (Herzschuh et al., 2016; Schurman et al., 2018).

Some previous studies have pointed to cumulative effects of multiple local impacts as the main or even unique causes behind *P. oceanica* loss, concluding that meadows may be recovered and managed through local actions (González-Correa et al., 2007; Boudouresque et al., 2009; Guillén et al., 2013; Telesca et al., 2015). Our results add up to this discussion and indicate that even though seagrass regression seems spatially variable, it cannot be only ascribed to local causes. This would reinforce Marbà et al. (2014) pointing to both, widespread disturbances acting at a local scale and long-term global disturbances, as factors behind *P. oceanica* loss. Additionally, local and global causes of seagrass regression seem to have spatially different relative weights, and the effect of their combined action seems, at least, additive.

Taking into account that our long-term data point to climate warming as a major driver of seagrass production and that the Mediterranean Sea is expected to be one of the regions most affected by human-induced warming in the next decades (Giorgi, 2006; IPCC, 2013), we could expect most Mediterranean seagrass meadows to continue declining. This supports Jordà et al. (2012), who stated that seagrass declining trends due to higher temperatures were found to be ineludible even if other local anthropogenic pressures were entirely mitigated. However, this decline most likely will not be spatially homogeneous, with some seagrass meadows being more vulnerable and degraded at faster rates than others, such as those in the Alboran Sea. On the other side, the long-term impact of climate change is not so evident in the sedimentary record of meadows located in the Cabrera Island. Their location could be a refuge from climate change, and local actions could be more effective there. It should also be considered that most of our cores were extracted at shallow and intermediate water depths. Therefore, the long-term impact of climate change on the lower limit of the meadows, more vulnerable as they are closer to the compensation depth, is not being addressed in our study. In other words, the overall long-term impact of climate might have even been more acute in deeper areas.

## 4.7. Managing seagrass habitats considering their long-term dynamics

Our paleoecological approach has provided specific information about the long-term stability of seagrass production for each meadow and the more probable causes of long-term change at a regional scale. Long-term data of the seagrass life-history that can help design more targeted management and conservation plans (Kilminster et al., 2015). Our results also revealed a significant long-term trade-off between the level of seagrass production and its temporal stability. The seagrass production stability over long term scales could decrease if managers only follow the criteria of maximising the level of seagrass production. Therefore, this information about the long-term stability should be taken into account in seagrass conservation and management plans aiming to increase their resilience (Kilminster et al., 2015), especially under the increasingly unstable future scenarios.

Following Game et al. (2008) considerations, the optimal strategy of conservation in ecosystems that are likely to spend more time in a degraded state, such as meadows along the more anthropised Andalusian coast, is to protect low-risk sites. Along Andalusia, the lowest-risk sites would be those meadows in their eastern side, that seem more resilient given their overall higher long-term temporal stability. However, in areas where meadows are under less stress, such as meadows in the Cabrera Island, it is best to take actions in the locations with higher risk. In Cabrera, that would correspond to the currently more impacted EP Bay. To sum up, the effectiveness of managing at a local-scale would more likely not be equal everywhere, because local and global impacts seem spatially different. The long-term data provided by paleoecological reconstructions can help in identifying those areas where local management could be more efficient.

## 5. CONCLUSIONS

This work demonstrates that FTIR is a powerful and useful method for paleoreconstructions in seagrass meadows, which in combination with other geochemical proxies and the multi-core approach used here, has allowed to get insights into the long-term seagrass processes and their dynamics. Our findings revealed key ecosystem processes, most of them associated with production, and provided a regional perspective for these processes.

Our study provides more reliable baseline data, helps to assess the magnitude of seagrass regression as well as elucidating the long-term causes behind seagrass decline, which seem spatially variable. We observed a common regressive trend of seagrass production in meadows located along the southern coast of Spain since AD ~1850-1900. Seawater warming, together with local impacts due to a highly anthropised coast, may have had a combined negative influence in the long-term seagrass production along the mainland coast. This pattern is not observed in meadows around the Cabrera Island, which could be due to geographical differences in seawater warming, together with more pristine conditions and a more central position in the species geographic range (and thus, natural environmental conditions). Our reconstruction contextualizes and helps to understand the differences in current seagrass decreasing trends. The present worse state of seagrass meadows along the mainland coast may be linked to the legacy of more conspicuous negative effects derived from past seawater warming and human impact. Further studies would be needed to confirm and assess the magnitude of the spatial differences in the influence of climate change in seagrass meadows along the Mediterranean.

## APPENDIX[3]

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[3] See supplementary materials in Appendix C.

# CHAPTER

# 4

# WHICH ENVIRONMENTAL FACTORS AFFECT LONG-TERM SEAGRASS CHANGES? THE RELATIVE IMPORTANCE OF LOCAL VERSUS LARGE-SCALE DRIVERS

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# ABSTRACT

The valuable seagrass ecosystems are worldwide and currently under regression. Human actions, of local and global scale, are widely accepted as the primary drivers behind seagrass decline. However, the interplay between local and large-scale drivers, over long periods of time, remains highly uncertain. A detailed long-term perspective of the drivers governing seagrass dynamics is most desirable to implement efficient meadow-specific management and conservation plans. Aiming at deciphering the weight of local and global drivers, we sampled sediment cores in seagrass meadows, mainly *Posidonia oceanica* (L.) Delile, and one meadow of *Cymodocea nodosa* (Ucria) Ascherson) along the coast of southeastern Spain and in the Balearic Islands, and analyzed them for elemental (XRF core scanner), isotopic (C and N) and spectral properties (FTIR-ATR). Data was summarized using principal components analysis (PCA), then generalized additive models (GAMs) were applied on the synthetic PCA variables to assess the effects of drivers on long-term seagrass production. We found evidence of multiple decisive contributors, although the balance between local and large-scale drivers varied spatially. Fluvial discharge exerted a ubiquitous, variable - with positive and negative impacts-, but moderate, influence. Seagrass meadows located at the westernmost geographical limit of *P. oceanica, grow in environments where* the higher river discharges and periodic upwelling events result in increased seawater turbidity, limiting light penetration. They were found to be less resilient to climate disturbances, and hence those more profoundly affected by global warming. On the other hand, the North Atlantic Oscillation mode had a significant influence, with overall higher production during negative phases - humid periods likely increasing nutrient availability due to enhanced terrestrial discharges and marine upwellings. Our data are not conclusive as to the effect of solar activity. These results suggest that the observed decline of *P. oceanica* meadows in its westernmost distributional area will likely be faster and accelerated under the scenario of increasing anthropic pressure over coastal environments.

# 1. INTRODUCTION

Seagrass meadows are critical coastal ecosystems whose first recorded losses started around AD 1850 (Marbà et al., 2005, 2014; de los Santos et al., 2019) and its worldwide decline accelerated since the 20th century (Waycott et al., 2009). In the Mediterranean basin, the endemic *P. oceanica* (L) Delile meadows have suffered deep losses with an overall rate of change of areal extent of -1.74% $\mathrm{yr}^{-1}$, a declining rate that almost doubles the -0.9% $\mathrm{yr}^{-1}$ estimated for seagrasses globally (Waycott et al., 2009; Marbà et al., 2014). Human actions, of local and global scale, are widely considered the major factors behind seagrass losses (Orth et al., 2006a; Boudouresque et al., 2009; Short et al., 2011; Marbà et al., 2014; Leiva-Dueñas et al., 2020b). However, few works have attempted to assess the relative magnitude of the different drivers governing long-term seagrass trends, and those that have done it covered small periods of time, reaching, at most, several decades being mainly focused on local environmental drivers (e.g. Kuo & Lin, 2010; Rasheed & Unsworth, 2011; Qiu et al., 2017; Shelton et al., 2017; Alonso Aller et al., 2019).

Seagrass meadows constitute highly dynamic ecosystems, responding to large-scale climate and local factors of both anthropic and natural origin. Currently, anthropogenic impacts of different scale are blurring natural seagrass variability (Duarte et al., 2006; O'Brien et al., 2018b). Major human impacts are attributed to widespread local disturbances, due to the increase of tourism and massive urbanisation along the coasts. Although they can also be of a broader spatial extent, such as the current climate change (Orth et al., 2006a; Boudouresque et al., 2009; Marbà et al., 2014; Leiva-Dueñas et al., 2020b).

There is a need for a more profound knowledge of seagrass long-term dynamics and drivers to design and implement efficient management and conservation plans. Past information can help comprehend present-day trends and improve ecosystem predictions (Willis et al., 2007; Davies & Bunting, 2010; Birks et al., 2012; Seddon et al., 2014b). However, current information on seagrass ecological trajectories does not go back beyond the AD 1850s (Marbà et al., 2005, 2014; Waycott et al., 2009). Moreover, and to our knowledge, the significance of the long-term disturbance drivers over centuries and millennia has not been assessed so far at a regional spatial scale. Long-term assessments are especially crucial for larger and long-lived species.

This is the case of *P. oceanica,* which requires decades to centuries to recover after a disturbance (González-Correa et al., 2005; Walker et al., 2006). Conservation and restoration actions would have higher chances of success if based on meadow-specific long-term diagnostics.

Long-term data from paleorecords provide insights into how the ecosystems responded to past changes. Luckily, some seagrasses, especially those of the *Posidonia* genus, promote the formation of sedimentary archives that can reach several meters in thickness, with a highly coherent chronological layering and a high temporal resolution (2-17 yr $cm^{-1}$) (e.g. Mateo et al., 2002; Serrano et al., 2016c; López-Merino et al., 2017; Lafratta et al., 2018). The information within these natural archives is an integration of all the past forcings and feedbacks (Bradley & Alverson, 2003; Seddon et al., 2014a). Therefore, the paleoinformation they contain can be useful to discriminate between the relative influence of the different drivers of disturbance.

Most seagrass sedimentary archives usually encompass the Late Holocene (last 4250 years; e.g. Mateo et al., 1997; Lo Iacono et al., 2008; López-Merino et al., 2015), although some of them may not go beyond the last few centuries (e.g. Mazarrasa et al., 2017a). Along the last centuries climate and human impact have highly interacted, therefore, separating the relative importance of natural versus anthropogenic forcings is a complex task. But assessing the relative importance of local versus large-scale drivers over time and space is still possible. By doing this, we may better understand why, along the Mediterranean coast, some seagrass meadows are declining faster than others and only a few of them show stable or even expanding area (Marbà et al., 2005, 2014; González-Correa et al., 2007; Guillén et al., 2013). Marbà et al. (2005) suggested that the imbalanced seagrass declines were a consequence of varying balances between anthropogenic versus climatic disturbances. They could not assess the different role between plausible causes and pointed to the need for long time series to evaluate it properly.

Here, we present a regional-scale assessment of the key environmental drivers regulating long-term seagrass production in different meadows located along southwest Mediterranean Sea. To achieve this goal, we sampled cores from seagrass deposits and used generalised additive models (GAMs), applied to synthetic variables obtained by principal component analyses, to assess the effects of local and large-scale environmental drivers on long-term seagrass production. The synthetic variables used as proxies of the seagrass production (i.e. the principal components) were mainly related to the abundance of seagrass macrodebris and a molecular composition characteristic of the seagrass organic matter (aromatics, phenols, carbohydrates and lipids) (Leiva-Dueñas et al., 2020b). This study constitutes a first step to quantitatively assess the partitioning between local and global factors explaining seagrass long-term changes at a regional scale. The specific objectives of this manuscript are to

i) identify the relative importance of local versus climate drivers in long-term seagrass production,

ii) describe the long-term relationships between seagrass production and the environmental drivers,

iii) and explore the regional spatial differences of local versus global (i.e., climate change) influence in long-term seagrass production.

## 2. MATERIALS AND METHODS

### 2.1. Study sites and field sampling

We sampled monospecific seagrass meadows along the Andalusian coast (southern Spain), and in two bays of the Cabrera Island, part of the Balearic Islands (eastern Spain) (Fig. 1). All seagrass meadows were formed by *P. oceanica*, except for a *C. nodosa* meadow (core BA, Table 1). We collected most cores at depths ranging between 0.5 and 10 m but for a transect at 5, 10, 15, and 25 m depth in Santa Maria Bay (SM) (Table 1). Seagrass meadows in Cabrera grow on biogenic, carbonate-rich and iron-deficient sediments, while in Andalusia, they grow over more terrigenous sediments (Marbà et al., 2005).

There are two different Mediterranean climates in the studied Andalusian coast. A subtropical type in the eastern side, characterised by lower temperatures and higher and more uniform precipitation along the year (mean annual temperature of 17.2 ºC and precipitation of 719 mm), while the westernmost area is characterised by a subdesertic climate (mean annual temperature of 17.6 ºC and precipitation of 236 mm; Liquete et al., 2005; CAGPD, 2014). Our study sites CA and ME are under the influence of the subtropical climate while RO, BA, AG, DE and TE are affected by the subdesertic climate. The climate in the Cabrera archipelago is semi-arid with a mean annual temperature of 14.6 ºC and precipitation of 375 mm (Alcover et al., 1993). Heavy episodic rainfalls are the main events supplying terrestrial sediment to these coastal areas.

The Alboran Sea (where CA, ME, RO and BA are located) has cold waters, showing very high productivity with elevated concentrations of Chl a. In contrast, the eastern side (where AG, DE and TE were sampled) has warmer waters with lower Chl a content (Ramírez et al., 2005; Muñoz et al., 2015). Coastal waters surrounding the Cabrera archipelago have a very low nutrient content compared to other coastal Mediterranean waters (Ballesteros & Zabala, 1993).

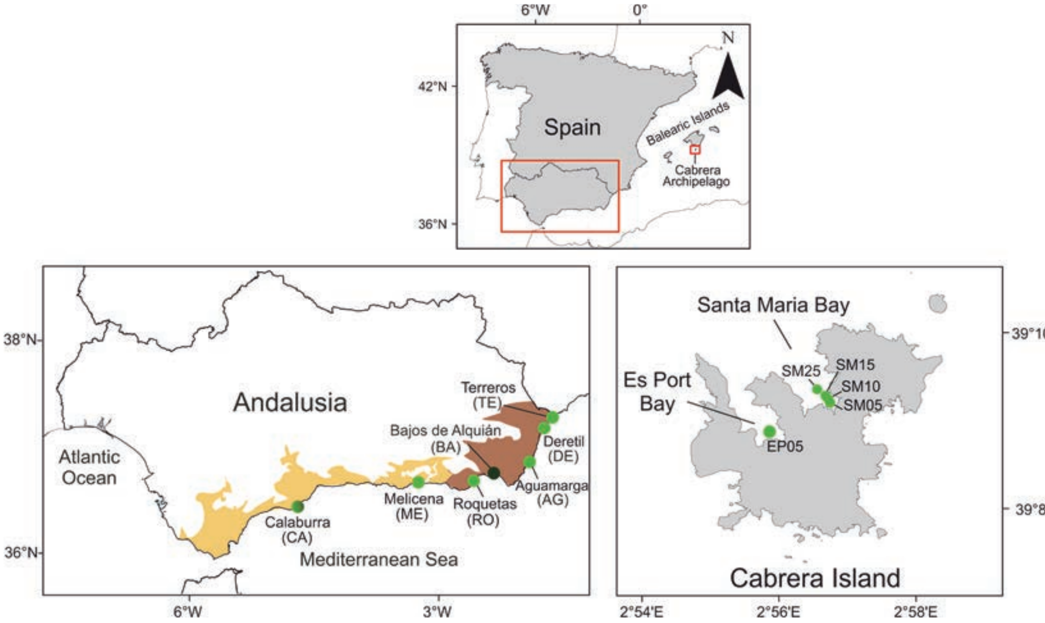


**Figure 1.** Location of the seagrass sediment sampling sites. Light green-coloured circles: *P. oceanica* meadows; Dark green circle: *C. nodosa* meadow. The numbers in Santa Maria Bay stand for the sampling depth (in meters). In Andalusia there are the two bioclimatic regions in the sampling area: subtropical Mediterranean (light orange) and subdesertic Mediterranean (light brown).

**Table 1**. Sampling sites details.

| **Region /Province** | **Location** | **Coordinates** | | **Water depth** (m) | **Seagrass species** | **Code** | **Core length** (cm) | **Comp.** (%) |
|---|---|---|---|---|---|---|---|---|
| Alboran, Málaga | Calaburras | 36°29'25.9"N | 4°41'37.25" W | 0.5 | *P. oceanica* | **CA** | 103 | 12.6 |
| Alboran, Granada | Melicena | 36°44'53.99"N | 3°14'3.78"W | 4.2 | *P. oceanica* | **ME** | 78 | 22.3 |
| Alboran, Almeria | Roquetas | 36°47'15.50"N | 2°35'20.10" W | 1.5 | *P. oceanica* | **RO** | 140 | 41.6 |
| Mediter., Almería | El Alquian | 36°49'39.1"N | 2°23'14"W | 6.8 | *C. nodosa* | **BA** | 117 | 9.8 |
| Mediter., Almería | Aguamarga | 36°56'15.66"N | 1°56'0.42"W | 4.8 | *P. oceanica* | **AG** | 173 | 13.1 |
| Mediter., Almería | Villaricos | 37°15'18.93"N | 1°45'29.53" W | 16 | *P. oceanica* | **DE** | 157 | 16 |
| Mediter., Almería | Terreros | 37°21'0.12"N | 1°40'36.37" W | 5.5 | *P. oceanica* | **TE** | 88 | 14.3 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39°9'0"N | 2°56'57"E | 5 | *P. oceanica* | **SM05** | 83 | 42 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39°9'3"N | 2°56'55"E | 10 | *P. oceanica* | **SM10** | 161 | 18 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39°9'6"N | 2°56'53"E | 15 | *P. oceanica* | **SM15** | 138 | 19 |
| Mediter., Cabrera Archipelago | Santa Maria Bay | 39°9'12"N | 2°56'44"E | 25 | *P. oceanica* | **SM25** | 89 | 5.6 |
| Mediter., Cabrera Archipelago | Es Port Bay | 39°8'42"N | 2°55'60"E | 5 | *P. oceanica* | **EP** | 98 | 17 |

Sediment coring was conducted in June 2015 in the Cabrera Island and in October 2016 and July 2017 along the Andalusian coast. SCUBA divers collected the samples using high-density PVC corers fitted with core catchers and serrated leading edge. An exponential decompression function was applied to correct for core shortening (Morton & White, 1997; Serrano et al., 2012). Detailed information about the environmental setting and sampling procedures can be found in Leiva-Dueñas et al. (2020b).

## 2.2. Laboratory analyses

Cores were cut longitudinally and opened in two halves. One-half of each core was analysed for elemental composition using an Avaatech XRF core scanner (CORELAB laboratory, University of Barcelona). Alternate one cm-thick subsamples were dried at 60ºC until constant weight. Seagrass organic debris larger than 2 mm (after sieving) were picked and weighted to obtain the coarse seagrass organic matter content (seagrass COM), and then returned to its sample, which was then homogenised using an agate mortar (Mortar Grinder RM-200 RETSCH, CEAB-CSIC). Total organic matter content (OM) was estimated by mass-loss-on-ignition at 450ºC for 5h. Carbon and N elemental and isotopic composition of sediment samples were analysed at UH Hilo Analytical Laboratory, University of Hawaii at Hilo, on a Thermo-Finnegan Delta V IRMS isotope ratio mass spectrometer coupled with a Costech elemental analyser.

FTIR spectra of the ground sediment samples were obtained using an FTIR-ATR spectrometer equipped with a single-reflection diamond crystal (Agilent Cary 630, EcoPast Lab, Universidad de Santiago de Compostela). Spectra were obtained in the mid-infrared region (4000-400 $cm^{-1}$) at a resolution of 4 $cm^{-1}$. Background acquisition was performed before each measurement and 200 scans were set to obtain every spectrum. The second derivative FTIR spectra were obtained for all samples and the second derivative sum spectrum was computed and used for wavelength peak selection ("andurinha" R package; Álvarez Fernández & Martínez Cortizas, 2020). The assignment of absorption peaks to specific inorganic and organic molecular structures was based on available literature (Table S3). All variables used in this study were previously published, therefore, detailed core opening, subsampling and analyses procedures can be found in Leiva-Dueñas et al. (2020b).

## 2.3. Seagrass deposits chronology

Samples of *P. oceanica* sheaths or *C. nodosa* debris were selected at 2-9 depths in each core and radiocarbon dated using an accelerator mass spectrometry (DirectAMS laboratory). The uppermost 30 cm of each core were dated by quantification of $^{210}$Pb activities using alpha spectrometry (Laboratori de Radioactivitat Ambiental, Universitat Autònoma de Barcelona). Both dating methods were combined to obtain age-depth models, developed using the Bayesian modelling approach *Bacon* (Blaauw & Christen, 2011) in the R statistical environment (version 3.6.0; R Core Team, 2019). Radiocarbon dating results and details can be consulted in Leiva-Dueñas et al. (2020b)

## 2.4. Statistical methods

All statistical analyses were conducted using R statistical software version 3.6.0 (R Core Team, 2019), using packages psych (Revelle, 2019), robCompositions (Templ et al., 2011), mgcv (Wood, 2011, 2017), itsadug (van Rij et al., 2017), and most figures were done using ggplot2 (Wickham, 2016).

### Summarising variables

Instead of using the measured variables directly in GAMs, they were first summarised through a PCA. Using principal components in generalised additive models (GAMs) can remove correlations between the variables, reduce noise, and balance the need for including all the important variables while removing the impact of high correlations. This is key in paleoecological studies where multiple variables are measured. Including all proxies in a model would cause overfitting due to a higher number of coefficients than data points. The resultant principal components (PCs) were used as response or explanatory variables in GAMs. Previous studies have proved the better performance of GAM models based on PCAs (Zhao et al., 2014). Like most other statistical modelling techniques, GAMs do not take into account the plausible measurement error of proxies and neither the uncertainty due to the age-depth models.

We run two PCAs including all measured variables, one for each area of study (Andalusia, Cabrera; Table 2, Fig. 2). Variables included in the PCAs were FTIR selected absorbances, XRF-measured elements (Si, S, Br, Ca, Fe, Ti, Cl, K, Mn), OM, Seagrass COM and stable carbon and nitrogen isotope ratios. Principal components interpreted as related to seagrass production were used as response variables while those related with other local processes (such as terrestrial influence or whole ecosystem production) were used as explanatory variables.

The interpretation of the principal components in Andalusia and Cabrera is the same as the one made in Leiva-Dueñas et al. (2020b). This is because the data used is the same except for the global climate variables not included in PCAs here, but this fact did not change the correlation of the rest of the variables.

Explanatory variables included terrestrial influence and ecosystem production as local influencing factors. They also included global climate variables: Total Solar Irradiance (TSI, Vieira et al., 2011), Northern Hemisphere Temperature (NHT, Kobashi et al., 2013), greenhouse gases (GHG, Kobashi et al., 2013), and the North Atlantic Oscillation, the primary climate mode explaining climate variability in the North Atlantic (NAO index; Hurrell, 1995, 2003; Trouet et al., 2009; Olsen et al., 2012).

Climate variables were also summarised by using PCA, which resulted in three principal components (Table 3). The first component ($PC1_{CLIM}$) had positive loadings for GHG and NHT. The main significant change of $PC1_{CLIM}$ scores is the exponential rise after AD 1900 (Fig. 3C), reflecting the recent rise of the global mean atmospheric temperature due to the unprecedented exponential increase in anthropogenic greenhouse gases in the atmosphere. $PC1_{CLIM}$ is thus related to the human influence on the global climate. The second component ($PC2_{CLIM}$) showed positive loadings for TSI and NHT. $PC2_{CLIM}$ is related to non-human induced climate changes because its loadings are associated with temperature changes due to the natural solar irradiance variability. The third component ($PC3_{CLIM}$) had a positive loading for the NAO index (Table 2, Fig. 3C).

Therefore, for every core, we ended up with a response variable (a principal component related to seagrass production) and several explanatory variables. Some explanatory variables were of local spatial scale (principal components related to terrestrial influence and ecosystem production), and others of a global/regional spatial scale ($PC1_{CLIM}$, $PC2_{CLIM}$ and $PC3_{CLIM}$).

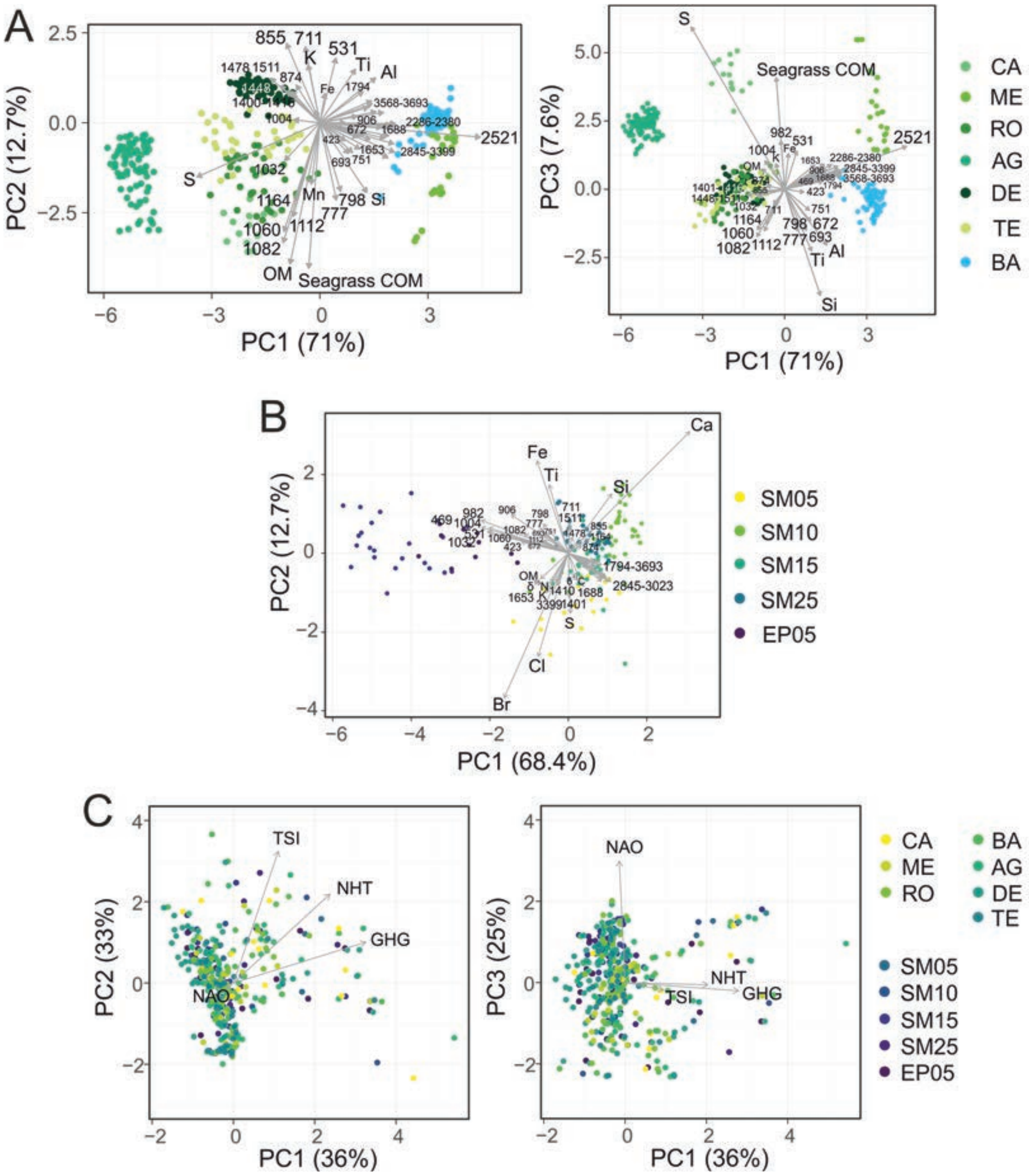


**Figure 2.** (A) and (B) Biplots for the analyzed variables from the cores (A) along the Andalusian coast ($PCA_{AND}$) and (B) in the Cabrera Island ($PCA_{CAB}$). Numbers correspond with wavelengths of FTIR absorbance; content of organic matter (OM), content of coarse organic matter from the seagrass (Seagrass COM), carbon and nitrogen stable isotopes, XRF-measured elements (Al, Fe, Si, Ti, K, Mn, Ca, Br, Cl, S). (C) Biplots for the global climatic variables: Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009) and Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013).

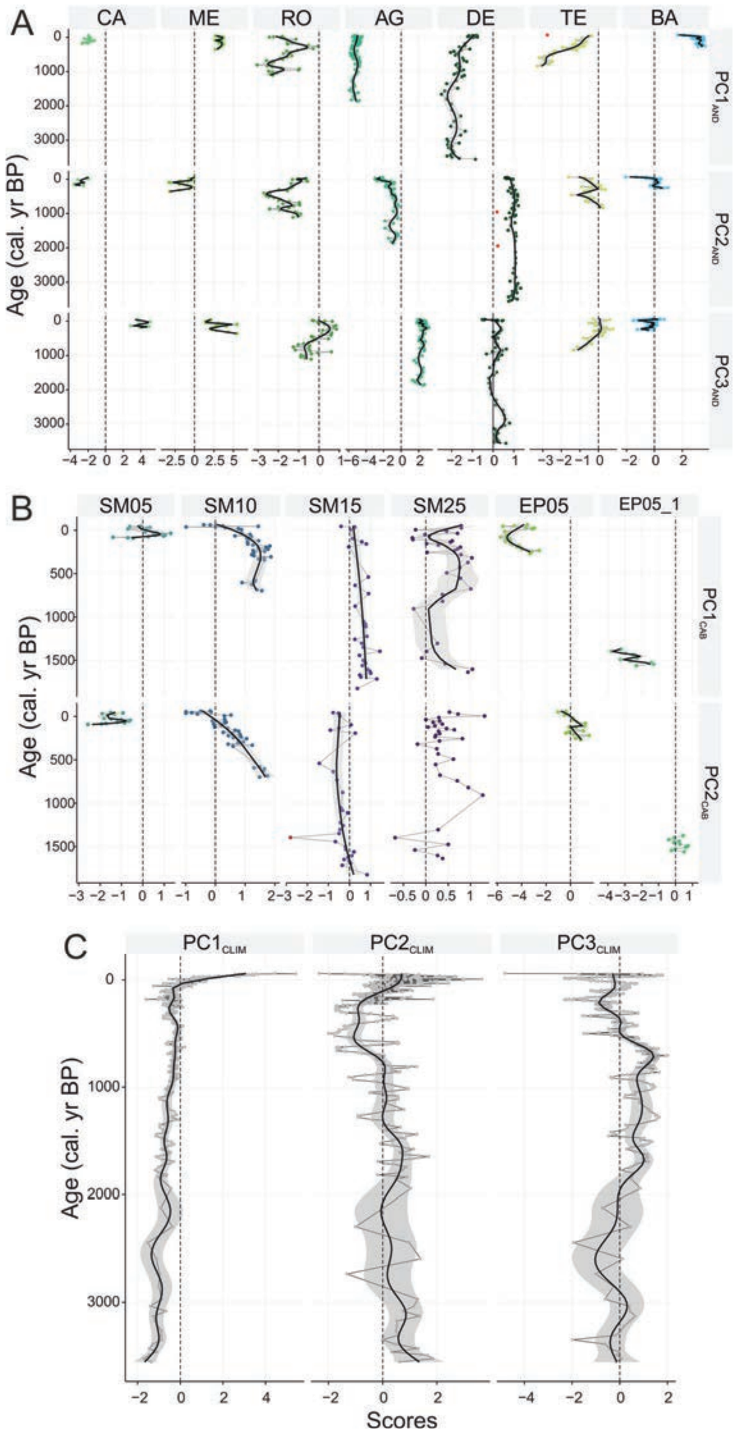


**Figure 3.** Depth records of the principal components scores obtained in PCA for the measured variables from cores (A) along the coast of Andalusia, (B) from the Cabrera Island and in PCA summarizing global climatic variables (C). Black solid lines indicate the fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant ($p < 0.05$) trends are shown.

**Table 2.** Factor loadings of the FTIR absorbances ($cm^{-1}$) and the other proxies used in $PCA_{SEAGRASS}$ with data from our cores. Numbers in bold indicate high factor loadings, while numbers in bold and italic indicate moderate factor loadings. OM: content of organic matter; Seagrass COM: weight of seagrass coarse organic matter.

| | ANDALUSIA | | | CABRERA | | | ANDALUSIA | | | CABRERA | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC1 | PC2 | | PC1 | PC2 | PC3 | PC1 | PC2 |
| | 71% | 12.7% | 7.6% | 68.4% | 12.7% | | 70% | 8.7% | 5.1% | 64.8% | 12.5% |
| **Al** | **0.14** | **0.12** | **-0.19** | -0.15 | 0.02 | **1112** | -0.07 | **-0.24** | **-0.14** | -0.08 | 0.04 |
| **Mn** | -0.02 | **-0.16** | 0 | -0.28 | 0.05 | **1164** | -0.06 | **-0.2** | **-0.12** | 0.07 | 0.05 |
| **Si** | **0.12** | **-0.18** | **-0.36** | **-0.26** | **0.04** | **1401** | -0.07 | 0.07 | -0.01 | 0 | **-0.14** |
| **S** | **-0.32** | **-0.14** | **0.55** | -0.09 | **0.02** | **1410** | -0.07 | 0.08 | -0.01 | -0.04 | **-0.1** |
| **K** | -0.03 | **0.15** | 0.09 | -0.09 | **0.05** | **1416** | -0.07 | 0.08 | -0.01 | -0.04 | -0.09 |
| **Ti** | 0.09 | **0.14** | **-0.21** | -0.01 | **0.1** | **1448** | -0.09 | 0.08 | -0.01 | 0.02 | -0.01 |
| **Fe** | 0.01 | 0.08 | **0.12** | **-0.08** | **0.04** | **1478** | **-0.1** | **0.1** | -0.02 | 0.01 | 0.05 |
| **Br** | - | - | - | **-0.1** | **0.06** | **1511** | **-0.13** | **0.11** | -0.02 | 0.01 | 0.09 |
| **Cl** | - | - | - | **-0.09** | **0.09** | **1653** | **0.1** | -0.07 | 0.08 | -0.07 | **-0.13** |
| **Ca** | - | - | - | **0.06** | **0.14** | **1688** | **0.16** | -0.01 | 0.08 | 0.05 | **-0.11** |
| **$\delta^{15}N$** | - | - | - | 0.04 | -0.01 | **1794** | **0.11** | 0.08 | 0.05 | **0.11** | -0.04 |
| **$\delta^{13}C$** | - | - | - | -0.19 | 0.11 | **2286** | **0.19** | 0 | 0.06 | 0.09 | -0.03 |
| **Seagrass COM** | -0.03 | **-0.37** | **0.38** | -0.28 | 0.08 | **2322** | **0.19** | -0.01 | 0.06 | 0.09 | -0.03 |
| **OM** | -0.08 | **-0.36** | 0.07 | -0.25 | 0.06 | **2348** | **0.18** | -0.01 | 0.07 | 0.09 | -0.04 |
| **423** | 0.07 | -0.05 | -0.01 | **-0.26** | 0.05 | **2380** | **0.18** | -0.01 | 0.08 | 0.08 | -0.04 |
| **469** | 0.06 | 0 | 0.03 | **-0.19** | 0.04 | **2521** | **0.41** | -0.04 | **0.15** | **0.1** | -0.04 |
| **531** | 0.04 | **0.17** | **0.13** | **-0.15** | 0.06 | **2845** | **0.19** | -0.08 | 0.05 | **0.14** | -0.09 |
| **672** | 0.09 | -0.02 | **-0.11** | -0.08 | 0.03 | **2881** | **0.17** | -0.09 | 0.05 | **0.14** | -0.09 |
| **693** | 0.07 | -0.08 | **-0.14** | 0.06 | 0.06 | **2902** | **0.18** | -0.09 | 0.05 | **0.13** | -0.09 |
| **711** | -0.04 | **0.2** | -0.05 | 0.02 | **-0.17** | **2922** | **0.11** | -0.03 | 0.04 | **0.11** | -0.09 |
| **751** | 0.08 | -0.08 | -0.07 | -0.03 | -0.14 | **2937** | **0.11** | -0.03 | 0.05 | **0.11** | -0.08 |
| **777** | 0.04 | **-0.2** | **-0.14** | -0.03 | -0.12 | **2955** | **0.17** | -0.04 | 0.05 | **0.12** | -0.08 |
| **798** | 0.05 | **-0.18** | **-0.12** | 0.01 | -0.01 | **2985** | **0.18** | -0.03 | 0.05 | **0.12** | -0.08 |
| **855** | -0.09 | **0.2** | -0.01 | 0 | 0.06 | **3004** | **0.19** | -0.05 | 0.05 | **0.11** | -0.07 |
| **874** | -0.06 | **0.1** | 0.01 | -0.01 | 0.09 | **3023** | **0.13** | -0.04 | 0.03 | **0.1** | -0.08 |
| **906** | **0.1** | 0.02 | 0.06 | **-0.05** | **-0.14** | **3399** | **0.1** | -0.04 | 0.04 | -0.05 | **-0.13** |
| **982** | -0.01 | 0.03 | **0.16** | **0.06** | **-0.1** | **3568** | **0.14** | 0.03 | 0.07 | 0.06 | -0.05 |
| **1004** | -0.07 | 0.01 | **0.1** | **0.11** | -0.02 | **3619** | **0.13** | 0.06 | 0.09 | 0.06 | -0.03 |
| **1032** | -0.09 | **-0.1** | -0.03 | **0.09** | -0.02 | **3632** | **0.13** | 0.05 | 0.08 | 0.07 | -0.03 |
| **1060** | -0.09 | **-0.28** | **-0.14** | **0.09** | -0.02 | **3650** | **0.12** | 0.04 | 0.07 | 0.08 | -0.02 |
| **1082** | -0.09 | **-0.31** | **-0.16** | **0.09** | -0.03 | **3693** | **0.16** | 0.03 | 0.06 | **0.1** | -0.03 |

**Table 3.** Factor loadings of the $PCA_{CLIMATIC}$ summarizing the global climatic variables. TSI: Total Solar Irradiance (Vieira et al., 2011); NAO: North Atlantic Oscillation (a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009); NHT: Northern Hemisphere Temperature (Kobashi et al., 2013).

| | GLOBAL CLIMATE | | |
|---|---|---|---|
| | $PC1_{CLIM}$ | $PC2_{CLIM}$ | $PC3_{CLIM}$ |
| | 36% | 33% | 25% |
| **NAO** | -0.05 | -0.04 | **1.00** |
| **TSI** | 0.32 | **0.93** | -0.06 |
| **NHT** | **0.68** | **0.63** | -0.02 |
| **GHG** | **0.93** | 0.29 | -0.07 |

## Generalised Additive Models

GAMs allow for non-linear relationships between the response variable and multiple explanatory variables. We use GAMs here because, as it happens with most populations in nature, seagrass ecological and metabolic processes show non-linear relationships with environmental variables (e.g., Koch et al., 2009; Villazán et al., 2016). Another advantage of using GAMs is that they provide temporal series of the contribution of the different covariates to the fitted response while other approaches such as variance partitioning analyses only report the overall amount of variance explained by each covariate (Simpson & Anderson, 2009). To evaluate the influence of several climatic and local variables on seagrass production, we started with a full model:

$$PC_{\text{Seagrass Production}} = \beta_0 + s(PC_{\text{Terr. infl.}}) + s(PC_{\text{Ecos. prod.}}) + s(PC1_{\text{CLIM}}) + s(PC2_{\text{CLIM}}) + s(PC3_{\text{CLIM}}) + \varepsilon$$

Where $\beta_0$ is the intercept, $\varepsilon$ is the error term, and each s(variable) represents a smooth function of the covariate. A Gaussian error distribution was used, and all model parameters were estimated using the GAM smoothing function with low-rank thin plate regression splines (Wood, 2003). To select the optimal smoothness parameters, we used the automatic restricted maximum likelihood smoothness selection (REML; Wood et al., 2016).

The final model for each core was selected using a backwards stepwise procedure, whereby we omitted an explanatory variable each time. We compared the fit of each of these reduced models with the full initial model by using a Likelihood ratio test and AIC statistics. The Likelihood ratio test checks whether dropping one term leads to a significant improvement in residual deviance. When this was the case, we proceeded to repeat this first step with the selected model until no significant improvement in residual deviance was achieved, meaning we reached the final model. We also calculated the contributions of the individual model covariates to the fitted values for each sediment sample. These contributions are calculated in practice using the function "predict.gam" (mgcv R package) and argument type= "terms". By doing so, we get temporal series of the effect of each explanatory variable on the response, effect that can vary through time, depending on the relationship between the variables and the response (Simpson and Anderson, 2009).

Model validation was carried out by checking plots of residuals versus fitted values, response versus fitted values, histograms of residuals and QQ-plots, so that we could verify the underlying assumptions of homogeneity and normality (Fig. S7). Most of the models did not violate these assumptions, at least seriously, except for sites CA and EP_1. The residuals of the models of these two locations were not normal, most probably because of the smaller sample size, so they must be interpreted with caution.

Because we deal with temporal series data, we also checked for residual autocorrelation. When there was a strong significant auto-correlation, we introduced an auto-correlation structure of type AR(1), because the significant lag term was always the first one. Final models did not show any residual autocorrelation (Fig. S8).

### Deviance partitioning

The deviance (also called residual deviance) of a GAM model is equivalent to the residual sum of squares, and the null deviance is the equivalent to the total sum of squares in linear regression. GAM models do not have an $R^2$, and the closest equivalent is the explained deviance, calculated as:

$$\text{explained deviance} = 100 \times \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}}$$

To determine the deviance explained by each term in every final model, we fitted several reduced models dropping out each term. After that, the deviance of the final model, the null model and reduced models were calculated. Using this information, we can calculate the deviance explained by a specific term as:

$$\text{Dev}(x_j) = 100 \times \frac{\text{Dev}(\text{model dropping } x_j) - \text{Dev}(\text{final model})}{\text{Dev}(\text{null model})}$$

## 3. RESULTS

GAM analyses explained between 20.3 and up to 99.7% of the deviance of the proxies of seagrass production (Table 4). Results of our GAM models indicated that among all the variables, the terrestrial influence was the only one explaining part of seagrass production at all sites, although the deviance explained was low to moderate (between 5 and 40%) (Table 4, Fig. 4A). There are negative associations between seagrass production and terrestrial influence at CA, ME, BA and SM05 stations while positive associations were found for the other sites, and almost all of these relationships with the terrestrial influence were linear (Fig. 5). The temporal series of the contribution of the terrestrial inputs on seagrass production (Fig. 6A, 6B) show a tendency towards negative contributions in some of the Andalusian and in the Cabrera Island meadows, especially during the first part (~650 to 400 cal yr BP) of the cold period known as the Little Ice Age (LIA), followed by a recovery towards more positive contributions over the second part of the LIA (400 to 150 cal. yr BP). At AG and DE, the cores covering longer periods, negative contributions of the terrestrial material can be observed starting around ~2200 cal. yr BP and until ~1500 cal. yr BP. After that period, terrestrial influence had more positive contributions until the start of the LIA, which is also observable at SM15 and SM25 (Fig. 6A, 6B).

As for the rest of explanatory variables, all of them affected seagrass production but not at all sites, showing diverse degrees of explained deviance. Each large-scale explanatory variable influenced six out of twelve cores. The explained deviances by $PC1_{CLIM}$ ranged from 23% to 53% (Table 4, Fig. 6A), and was correlated negatively with seagrass production along the Andalusian coast at sites CA, ME, TE and BA. For most of them, $PC1_{CLIM}$ showed a trend towards negative contribution since AD ~1850 (Fig. 6A). These relationships were mostly non-linear, again probably due to low observation frequency at the ends except for CA, where there is an inverted U-shape relationship (Fig. 5A). This U-shape relationship suggests that there is a threshold, so an increase in temperature may benefit the production of the seagrass to a certain point, beyond which the effect becomes negative. On the other hand, in the Cabrera Island, at SM10 and EP, $PC1_{CLIM}$ was positively correlated with seagrass production (Fig. 5B), showing a trend towards positive contributions since AD ~1850 (Fig. 6B).

The $PC2_{CLIM}$ had explained deviances ranging from 8% to 60% (Table 3, Fig. 5A), and was linearly correlated both positively (at CA, SM10) and negatively (at TE and SM15) with seagrass production. $PC2_{CLIM}$ did also show non-linear, inverted U-shaped relationships for BA and SM25 (Fig. 5). There is no common trend in the contribution of $PC2_{CLIM}$ with time (Fig. 6A, 6B).

$PC3_{CLIM}$, related with changes in NAO, had an explained deviance ranging between 13 to 53% (Table 3, Fig. 6A). Most of the relationships between $PC3_{CLIM}$ and seagrass production were negative (except for CA) and overall linear (except for CA and SM10), indicating higher seagrass production in negative phases of NAO (Fig. 5). The temporal series of the contribution of NAO ($PC3_{CLIM}$) on the Andalusian seagrass production ($PC3_{AND}$) revealed more positive contributions to seagrass production during the LIA, a cold and wet period in Iberia with lower values of NAO index (Fig. 6A). At SM10, the relationship between NAO and seagrass production is more concave-shaped, but overall the higher values of seagrass production happen during negative phases of NAO. The non-linear shape could be due to high uncertainties at the ends due to lower observation frequency (Fig. 5A).

The production at the ecosystem level only affected seagrass production at two sites: at BA and AG with 6% and 20% of explained deviance, respectively (Table 4, Fig. 6A). It showed a positive relationship at AG and after reaching saturation the relationship started to decline (Fig. 5A). At both sites, higher ecosystem production seems to have affected seagrass production negatively during the last century (Fig. 6A).

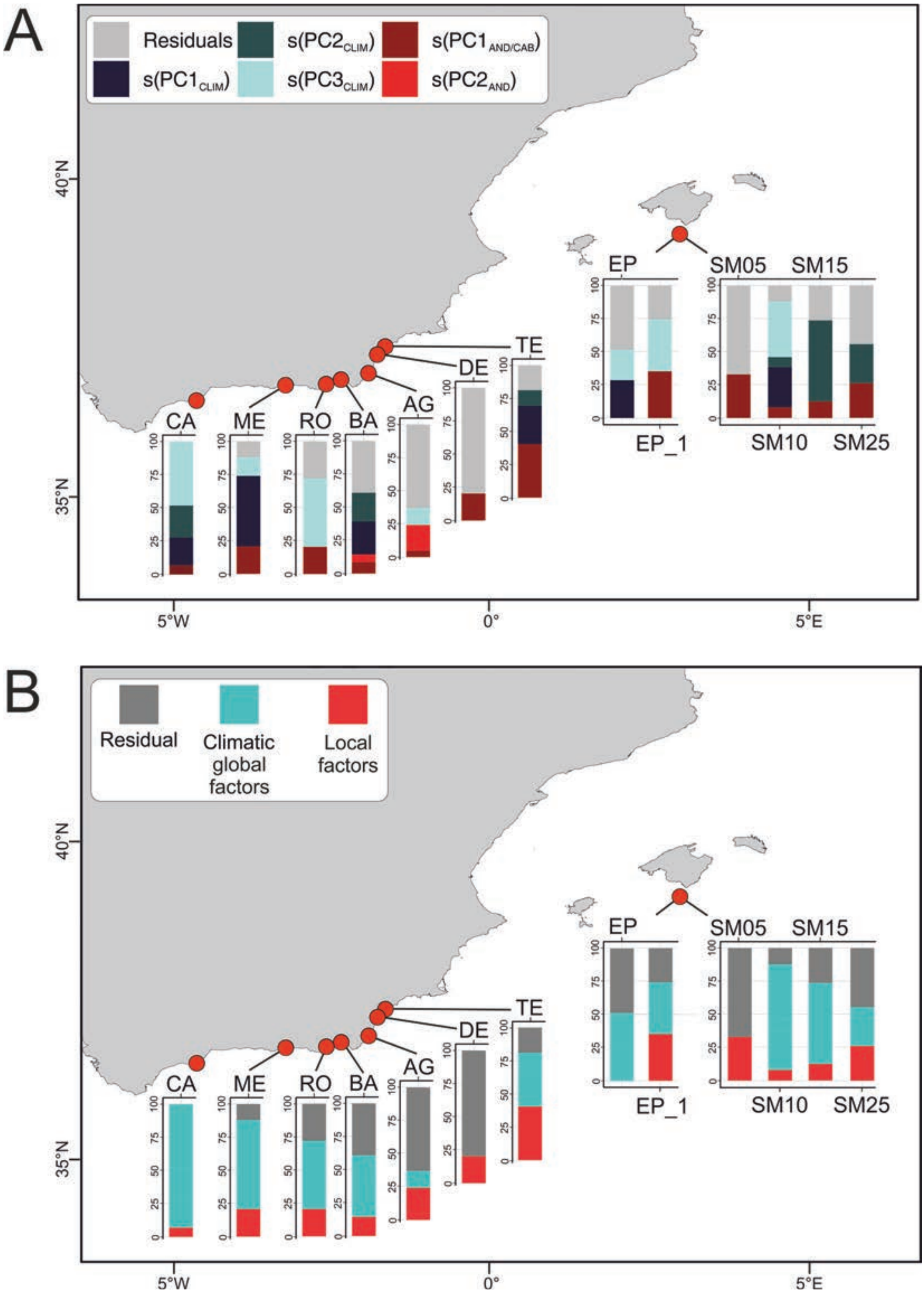


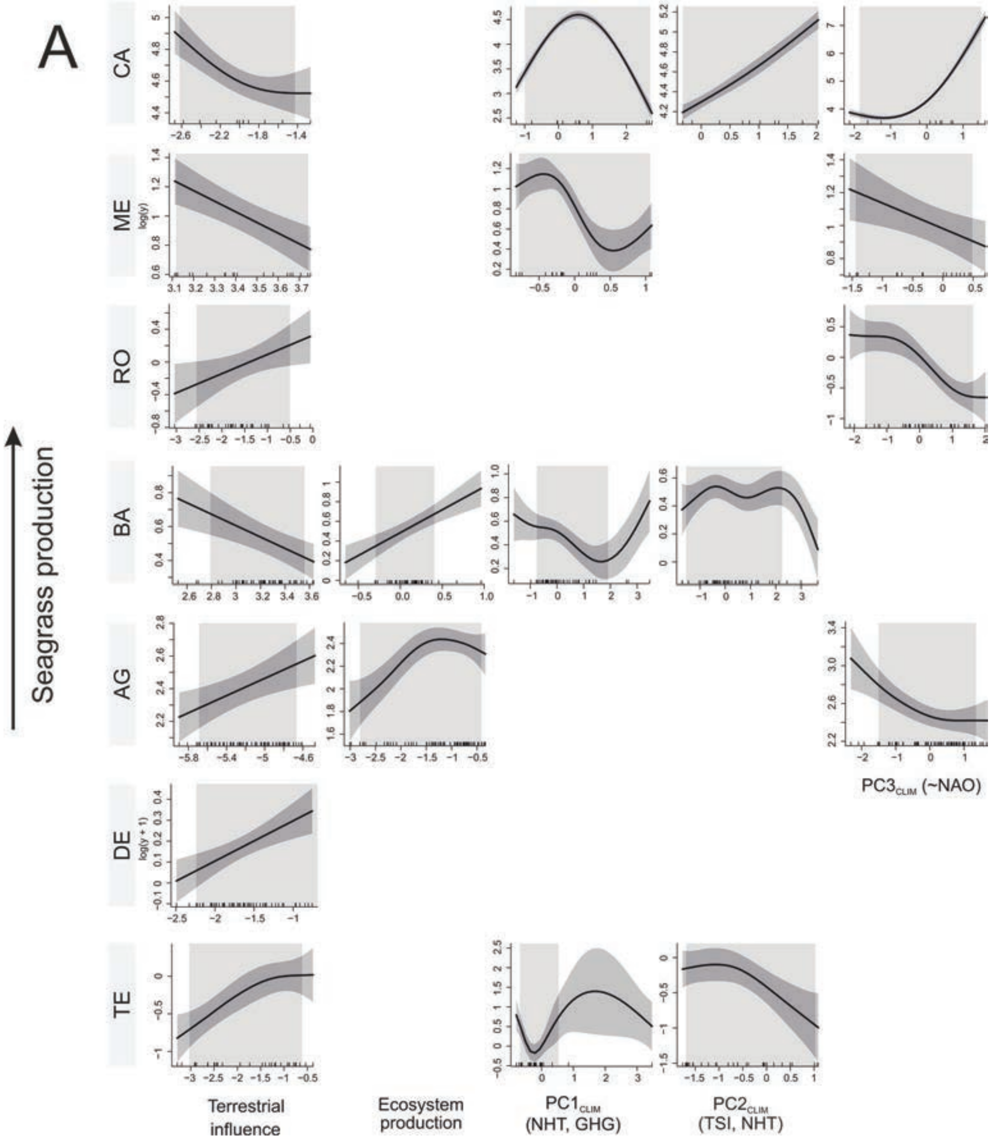
**Figure 4**. (A) Explained deviance by each term and residuals of every final full GAM model. (B) Explained deviance by terms grouped in global climatic and local factors, as well as residuals of every final full GAM model.

**Table 4.** Summary of the Estimated Effects of the Predictors for every model (one per core).

|  | **Deviance explained (%)** | **Sample size (n)** | **Smoothing terms** | **edf** | **Res.df** | **F** | **p-value** |  | **Deviance explained by term (parts per unit)** |
|---|---|---|---|---|---|---|---|---|---|
| CA | 99.70% | 12 | $s(PC1_{AND})$ | 1.882 | 1.986 | 17.55 | 0.0125 | * | 0.077 |
|  |  |  | $s(PC1_{CLIM})$ | 1.998 | 2 | 262.04 | $\ll 0.0001$ | *** | 0.231 |
|  |  |  | $s(PC2_{CLIM})$ | 1.668 | 1.89 | 100.27 | $\ll 0.0001$ | *** | 0.266 |
|  |  |  | $s(PC3_{CLIM})$ | 1.998 | 2 | 412.37 | $\ll 0.0001$ | *** | 0.529 |
| ME | 86.90% | 19 | $s(PC1_{AND})$ | 1 | 1 | 17.609 | 9.50E-04 | *** | 0.208 |
|  |  |  | $s(PC1_{CLIM})$ | 3.256 | 3.613 | 10.956 | 3.05E-04 | *** | 0.531 |
|  |  |  | $s(PC3_{CLIM})$ | 1 | 1 | 6.889 | 0.02098 | * | 0.142 |
| RO | 72.10% | 39 | $s(PC1_{AND})$ | 1 | 1 | 4.956 | 0.0326 | * | 0.205 |
|  |  |  | $s(PC3_{CLIM})$ | 3.057 | 3.865 | 9.978 | $\ll 0.0001$ | *** | 0.515 |
| BA | 62.70% | 53 | $s(PC1_{AND})$ | 1 | 1 | 12.336 | 0.00107 | ** | 0.086 |
|  |  |  | $s(PC2_{AND})$ | 1 | 1 | 22.012 | $\ll 0.0001$ | *** | 0.058 |
|  |  |  | $s(PC1_{CLIM})$ | 4.361 | 5.359 | 5.081 | 0.00077 | *** | 0.248 |
|  |  |  | $s(PC2_{CLIM})$ | 4.767 | 5.803 | 2.987 | 0.0182 | * | 0.216 |
| AG | 36.10% | 79 | $s(PC1_{AND})$ | 1 | 1 | 8.301 | 0.00519 | ** | 0.047 |
|  |  |  | $s(PC2_{AND})$ | 2.865 | 3.588 | 7.686 | $\ll 0.0001$ | *** | 0.195 |
|  |  |  | $s(PC3_{CLIM})$ | 2.387 | 3.025 | 6.35 | 0.00066 | *** | 0.128 |
| DE | 20.30% | 60 | $s(PC1_{AND})$ | 1 | 1 | 12.8 | 0.00069 | *** | 0.203 |
| TE | 84% | 33 | $s(PC1_{AND})$ | 1.984 | 2.449 | 17.014 | $\ll 0.0001$ | *** | 0.404 |
|  |  |  | $s(PC1_{CLIM})$ | 4.475 | 5.259 | 5.975 | 0.00071 | *** | 0.289 |
|  |  |  | $s(PC2_{CLIM})$ | 2.419 | 2.944 | 6.235 | 0.00312 | ** | 0.117 |
| SM05 | 32.90% | 17 | $s(PC1_{CAB})$ | 1 | 1 | 7.371 | 0.0157 | * | 0.329 |
| SM10 | 87.60% | 34 | $s(PC1_{CAB})$ | 1 | 1 | 4.109 | 0.0539 | . | 0.08 |
|  |  |  | $s(PC1_{CLIM})$ | 2.161 | 2.628 | 19.195 | $\ll 0.0001$ | *** | 0.302 |
|  |  |  | $s(PC2_{CLIM})$ | 1 | 1 | 24.657 | $\ll 0.0001$ | *** | 0.076 |
|  |  |  | $s(PC3_{CLIM})$ | 5.195 | 6.175 | 10.356 | $\ll 0.0001$ | *** | 0.42 |
| SM15 | 73.70% | 26 | $s(PC1_{CAB})$ | 2.683 | 3.279 | 3.019 | 0.0564 | . | 0.125 |
|  |  |  | $s(PC2_{CLIM})$ | 3.343 | 4.124 | 10.383 | $\ll 0.0001$ | *** | 0.611 |
| SM25 | 55.50% | 32 | $s(PC1_{CAB})$ | 1 | 1 | 17.73 | 0.00024 | *** | 0.262 |
|  |  |  | $s(PC2_{CLIM})$ | 3.889 | 4.793 | 3.499 | 0.01704 | * | 0.294 |
| EP | 51.40% | 20 | $s(PC1_{CLIM})$ | 1 | 1 | 10.637 | 0.00465 | ** | 0.285 |
|  |  |  | $s(PC3_{CLIM})$ | 1.739 | 2.178 | 2.962 | 0.06921 | . | 0.229 |
| EP_1 | 74.30% | 11 | $s(PC1_{CAB})$ | 2.253 | 2.698 | 3.826 | 0.0693 | . | 0.353 |
|  |  |  | $s(PC3_{CLIM})$ | 1.468 | 1.773 | 5.275 | 0.0337 | * | 0.391 |

Note. EDF = estimated degrees of freedom; Res. dF = residual degrees of freedom.

When we sum up the explained deviance by local factors (terrestrial influence and ecosystem production) and by climate variables ($PC1_{CLIM}$, $PC2_{CLIM}$, $PC3_{CLIM}$), the results showed that the influence of local factors is low to moderate at all sites. In contrast, global climate influence is not that widespread, but it did explain a higher deviance of seagrass production at some sites (Table 4, Fig. 4B). In fact, global climate influence is significantly higher for meadows whose cores cover shorter time spans ($R^2 = 0.59$, p-value = 0.003), have higher mean accumulation rates ($R^2 = 0.60$, p-value = 0.003) and lower model residuals ($R^2 = 0.78$, p-value = 0.0001) (Fig. S9). Local influence is lower in cores from meadows with higher mean accumulation rates ($R^2 = 0.37$, p-value = 0.035) and is mainly related with the terrestrial influence ($R^2 = 0.44$, p-value = 0.02) (Fig. S9).



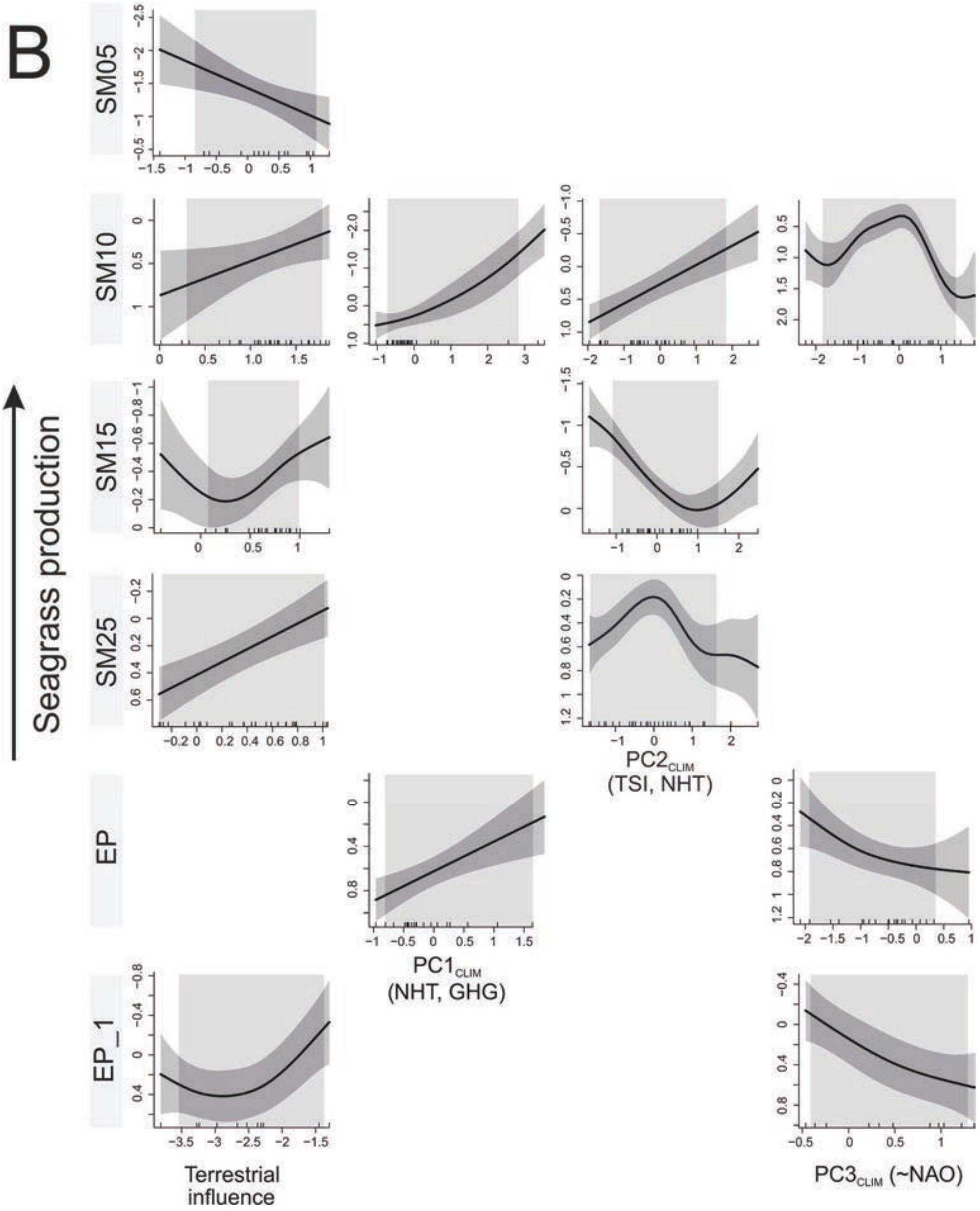
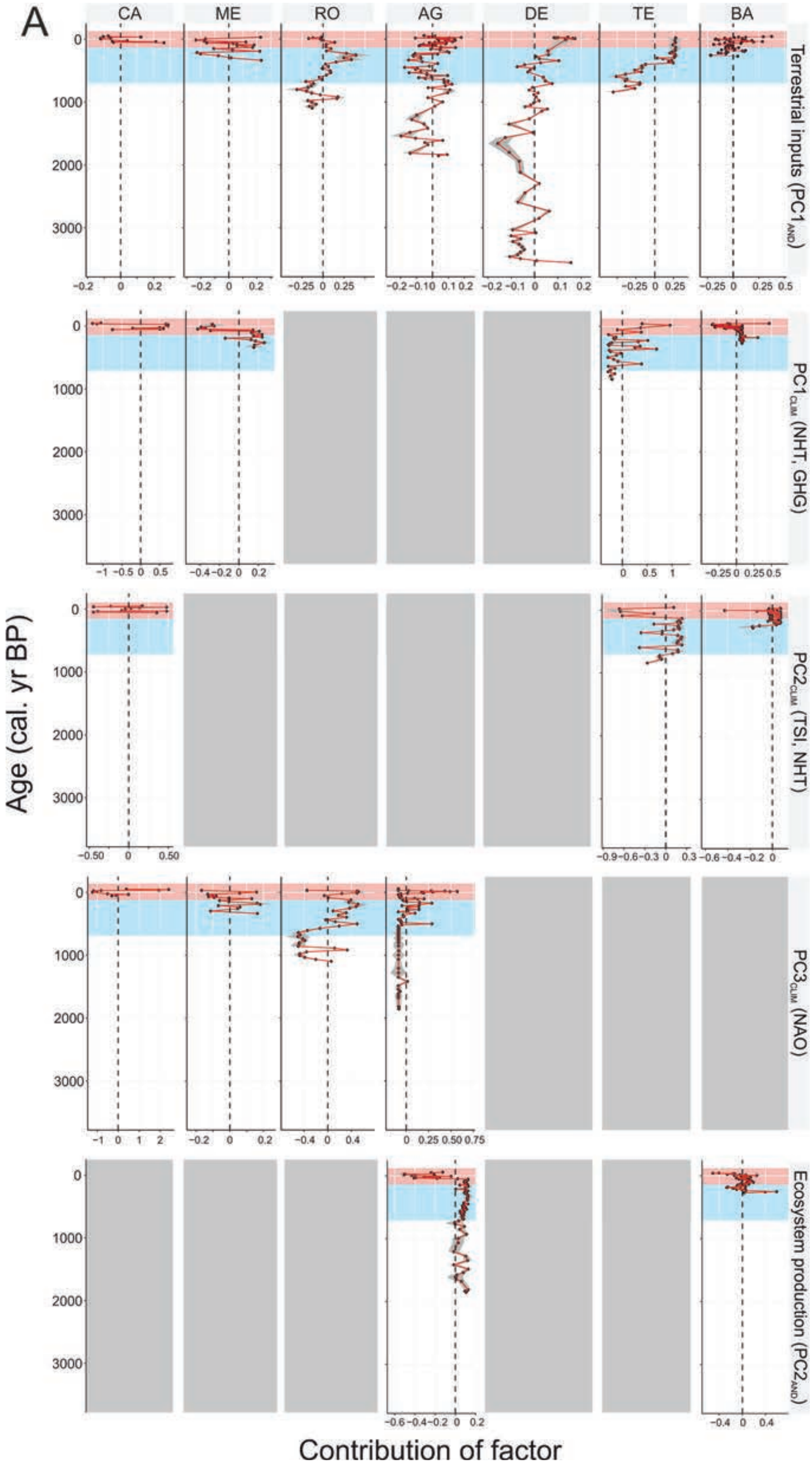


**Figure 5.** Generalized Additive Models partial effect splines for explanatory variables of every core located at (A, previos page) Andalusia and (B) Cabrera Island. Black thick lines indicate the value of the smoothing response, dark grey areas represent the 95% confidence intervals and shaded light grey areas correspond to middle 90% of all observations. The rugs on the x axis are the data points.


A
CA
ME
RO
AG
DE
TE
BA
Terrestrial inputs (PC1$_{AND}$)
PC1$_{CLIM}$ (NHT, GHG)
PC2$_{CLIM}$ (TSI, NHT)
PC3$_{CLIM}$ (NAO)
Ecosystem production (PC2$_{AND}$)
Age (cal. yr BP)
0
1000
2000
3000
Contribution of factor
-0.2 0 0.2
-0.2 0 0.2
-0.25 0 0.25
-0.2 -0.10 0.1 0.2
-0.2 -0.1 0 0.1 0.2
-0.25 0 0.25
-0.25 0 0.25 0.5
-1 -0.5 0 0.5
-0.4 -0.2 0 0.2
0 0.5 1
-0.25 0 0.25 0.5
-0.50 0 0.50
-0.9 -0.6 -0.3 0 0.3
-0.6 -0.4 -0.2 0
-1 0 1 2
-0.2 0 0.2
-0.4 0 0.4
0 0.25 0.50 0.75
-0.6 -0.4 -0.2 0 0.2
-0.4 0 0.4

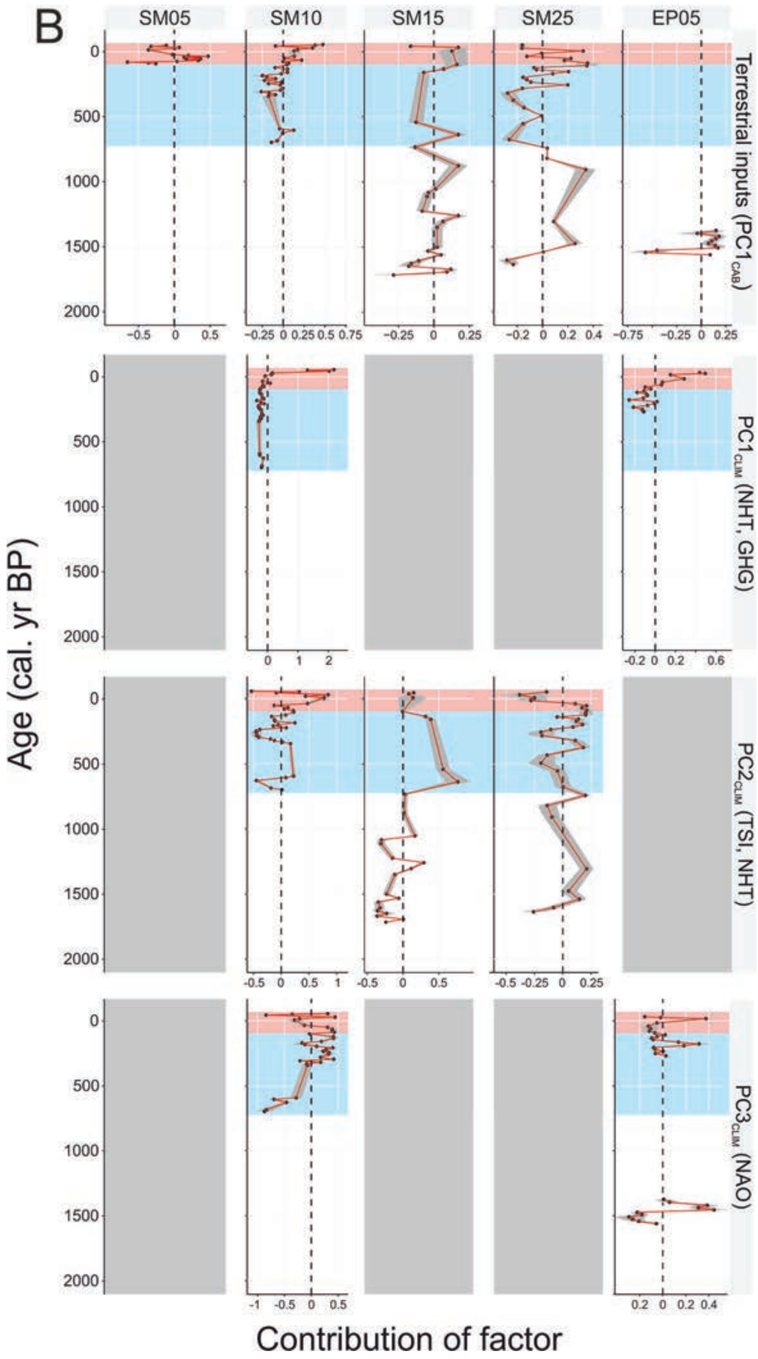


**Figure 6.** The contribution of the different driving environmental factors considered to the fitted PCA scores related to seagrass production for cores located at (A, previous page) Andalusia and (B) Cabrera for their final GAM models. The grey band is an approximate 95% pointwise confidence interval on the contribution. Where the band includes the dashed zero line, the contribution of the covariate is not statistically significantly different from the intercept. Light red area highlights the recent warming period observed in Alboran SST records and the light blue area indicates the Little Ice Age period.

# 4. DISCUSSION

## 4.1. Influence of local factors on seagrass production

Two explanatory variables related to local factors were included in our models: the influence of terrestrial material ($PC1_{AND}$ and $PC1_{CAB}$) and the production at the ecosystem level ($PC2_{AND}$). Both were obtained by summarising all the proxies measured in our cores. The main influencing local factor was the influx of terrestrial material, with a ubiquitous influence, while the ecosystem production explained some variability in a few sites.

### Terrestrial inputs

The fluxes of terrestrial material from the adjacent catchment to the coastal area usually result in a simultaneous increase in water turbulence, sedimentation rates and nutrient loads (Ralph et al., 2006; Erftemeijer & Lewis, 2007). All of them affect light penetration negatively and light is considered the primary environmental variable affecting seagrass distribution (Lee et al., 2007; Ralph et al., 2007). Therefore, its attenuation restricts photosynthesis and hence seagrass production (Magris & Ban, 2019). If nutrient levels are high, algal blooms could occur because algae are more efficient at high nutrient concentration levels. These blooms further suffocate seagrasses mainly by shading and limiting underwater light availability (McGlathery, 2001; Burkholder et al., 2007; McGlathery et al., 2007). Moreover, *P. oceanica* is very sensitive to sediment burial even under moderate levels and short-time events (Manzanera et al., 2011). Overall, increased sediment run-off seems to affect seagrass production negatively. However, our results showed that the degree and the direction of the impact of terrestrial fluxes varied between sites. Due to the correlative and paleoecological nature of this study, it remains unclear which are the critical thresholds for the studied environmental factors, (such as terrestrial fluxes or any other driver), that surpass critical physiological limits leading to seagrass decline.

A significant negative correlation between the influence of terrestrial inputs on the seagrass production and sediment accumulation rates indicates that terrestrial fluxes had a negative impact in meadows with higher sediment accumulation rates (CA, ME, BA and SM05; Fig. S9). CA and ME are located on the western side of the Andalusian Mediterranean coast. This area has nutrient-rich waters due to periodic upwelling events and receives higher river water discharges because of the wetter climate (Macías et al., 2007; CAGPDS, 2014). The meadow in BA is located near the Andarax river, the Mediterranean river in Andalusia transporting more sediment per water discharge (Liquete et al., 2005). Seawaters are naturally more turbid in these meadows, hence, seagrasses are likely closer to their compensation point. In these cases, seagrass production can be more readily affected by any further reduction in seawater light due to enhanced river discharges. The negative relationship between seagrass production and terrestrial inputs seems to be related to the environmental setting, which favours the arrival of higher sediment loads and nutrient-enriched waters. Terrestrial inputs enhance seagrass production in meadows where sediment accumulation rates are lower (RO, AG, DE, TE, SM10, SM15, SM25, and EP). This is likely indicating a beneficial effect due to moderate nutrient inputs. Increased nutrient inputs can enhance seagrass production, especially if the meadows are nutrient-limited (McGlathery et al., 2007).

In cores encompassing longer periods, AG and DE, the terrestrial influence had a contribution towards negative values between ~2200-1500 cal. yr BP. Considering the positive relationship between seagrass production and terrestrial inputs in AG and DE (Fig. 5A), these negative contributions are very likely due to lower terrestrial inputs ($PC1_{AND}$, Fig. 3) which mostly coincides with the most humid and warm phase in southern Iberia, the Iberian Roman Humid Period (IRHP, 1450/1600 to 2500/2600 cal. yr BP; Martin-Puertas et al., 2009, 2010; Mesa Fernández et al., 2018). This humid phase has been described in marine and lacustrine records due to the conjunction of higher fluvial activity indicated by higher arrival of terrestrial elements and higher Mediterranean forest cover indicated by increases in the arboreal pollen (Martin-Puertas et al., 2009, 2010; Mesa Fernández et al., 2018; Ramos-Román et al., 2018a). It could be that at AG and DE locations (areas with semi-arid conditions) the increase of the regional Mediterranean forest was favoured by the wetter conditions during this phase, what may have helped to stabilise the soils, preventing their erosion and diminishing the terrestrial inputs into the coastal seagrass meadows. Lower detritic inputs associated with afforestation were also observed in a lake located close to the study area (Ramos-Román et al., 2018b). Both, negative and positive contributions from terrestrial inputs are observed in Andalusia throughout the LIA (~150-650 cal. yr BP), with negative contributions (lower terrestrial inputs) during the first half and positive contributions (higher terrestrial inputs) during the second half, in most cores. The LIA is an overall cold and humid period in Iberia and its southern region (Nieto-Moreno et al., 2013; Oliva et al., 2018). However, Nieto-Moreno et al. (2011) identified arid conditions during most of the first half of this period (from 650 to 450 cal. yr BP) in southern Iberia, which is in agreement with the lower terrestrial inputs captured by our records.

### The ecosystem production: interaction with other producers

Ecosystem production, the other local factor considered in our models, had an overall positive influence on seagrass production in cores BA and AG. The positive relationship could be simply indicating that the seagrass largely dominates the overall ecosystem production. It could also mean that there are positive seagrass-algae interactions, i.e. the combination of certain primary producers in the community may favour the seagrass production. Alexandre et al. (2017) found several positive seagrass-algae interactions, in which the collective nitrogen uptake was higher than in monospecific incubations, suggesting a benefit from macrophyte diversity in seagrass ecosystems. However, at AG the positive interaction seems limited until a certain point, after which, increases in the overall ecosystem production are no longer coeval with increases in seagrass production (Fig. 5A). This threshold could be related to algal blooms. Under excess of algae proliferation, the ecosystem production is no longer driven by the seagrass performance, which can be impaired by the light decrease due to the algae overgrowth (McGlathery et al., 2001, 2007).

## 4.2. Influence of global climatic factors on seagrass production

### The rise of temperature due to global warming

The $PC1_{CLIM}$, related with the increase of temperature linked with the rise in greenhouse gases emissions during the last centuries, has mostly negative relationships with seagrass production and significant negative contributions during the last 150 years in some sites from Andalusia (CA, ME and BA; Fig. 5A and 6A), but positive relationships with seagrass production and positive contributions during the last 150 years in sites from Cabrera Island (SM10, EP; Fig. 5B and 6B). The main difference between CA, ME and BA sites in Andalusia and SM10 and EP in Cabrera is that terrestrial inputs negatively influence seagrass production in the Andalusian meadows while in the Cabrera island the river runoff has a positive influence. This opposite reaction to human-induced temperature rise could be the result of combined, even synergic, adverse effects from terrestrial inputs and the temperature rise in the Andalusian sites. Seagrass photosynthesis has maximum rates at an optimum temperature, above which the photosynthetic rates decline. Otherwise, respiration increases continuously as temperature increases, which may end in negative carbon balance and growth above certain temperature thresholds (Collier et al., 2011). CA, ME and BA are shallow seagrass meadows usually growing naturally at warmer temperatures compared to deeper areas. Seagrass growth at higher temperatures is limited. It is suggested that under warmer conditions, seagrasses need more light to maintain positive carbon balances (Lee et al., 2007; Collier et al., 2011). However, the very high terrestrial fluxes may reduce light availability in these sites. The lower photosynthesis due to their natural low light conditions and the enhanced respiration due to the recent seawater warming is likely to have caused negative carbon balances. Consequently, it seems that meadows such as CA, ME and BA receiving higher river runoff and hence, with reduced underwater light, are more susceptible to the increase in seawater temperature due to the actual scenario of global warming than other Andalusian meadows with lower terrestrial inputs. These findings are consistent with previous research, which observed that seawater warming and other local stressors (such as nutrient or organic matter enrichment, light reduction, and changes in salinity) had combined negative (synergistic or additive interactions) effects on seagrasses (Collier et al., 2011; York et al., 2013; Salo & Pedersen, 2014; Moreno et al., 2018; Ontoria et al., 2019a, 2019b).

In Cabrera, the lower terrestrial inputs (the size of the catchments in the island is rather small compared to those in the mainland) did not have detrimental effects on seagrass production in most meadows, as previously discussed. Therefore, light availability and photosynthesis are not as reduced as in the Andalusian meadows, and seagrass meadows growing under higher light conditions, like those in Cabrera, have more optimal temperatures for photosynthesis. This might explain why the temperature rise during the last 150 years, due to global warming, did not have a negative effect in Cabrera. However, the optimum temperature for Cabrera meadows might have been recently overpassed given the negative seagrass growth, and the seagrass decline observed in the island within the last decades, steep declines coupled to seawater warming (Marbà & Duarte, 2010). Seawater warming was also previously identified as a driver of recent seagrass mortality in another meadow located in Mallorca by Díaz-Almela et al. (2009).

### The North Atlantic Oscillation

In six out of twelve meadows, both from Andalusia and the Cabrera Island, the North Atlantic Oscillation (NAO) atmospheric mode had a significant influence on seagrass production. The large influence of this index agrees with the fact that past and present-day climate in the southern Iberian Peninsula is particularly influenced by fluctuations of NAO, mainly regarding wind patterns and the intensity and distribution of precipitation (Rodrigo et al., 2000; Mayewski et al., 2004; Trigo et al., 2004; Frigola et al., 2007; Fletcher & Zielhofer, 2013; Schirrmacher et al., 2019). Our results indicated that lower values of this mode are coeval with increases in seagrass production. Negative NAO phases are associated with low atmospheric pressure, more humid conditions and stronger westerlies influence over southern Iberia (Hurrell, 1995; Rodrigo et al., 2000; Trigo et al., 2004). During low NAO index years, north-westerly winds are weaker and, consequently, are southward displaced to mid-latitudes. As a result, westerlies prevail in the Alboran Sea and cause a faster inflow of the Atlantic surface water current, leading to increased vertical mixing, gyre-induced upwellings of nutrient-rich deeper waters and increased primary productivity (Moreno et al., 2005; Ausin et al., 2014). A higher seagrass production during these negative NAO phases, under wetter conditions, could be explained due to higher availability of nutrients, either from enhanced upwelling events, higher river discharges of terrestrial material, or both. This link was already described in Leiva-Dueñas et al. (2020b) through multivariate explanatory statistical analyses and is confirmed here by GAMs models. Higher ocean paleoproductivity during periods of low atmospheric pressure and enhanced surface water mixing in the Alboran Sea has also been observed by Moreno et al. (2004), Ausin et al. (2014), and Schirrmacher et al. (2019). At decadal scales, several studies have demonstrated the influence of the NAO index on seagrass (Peirano et al., 2011) and marine macroalgae changes in the Mediterranean Sea (Melero Jiménez et al., 2017)

## The global solar irradiance

There is a high variability regarding the relationship between solar irradiance and its associated changes in temperature ($PC2_{CLIM}$) and seagrass production. There are linear positive and negative relationships but also uni- and bimodal relationships (Fig. 5A, 5B). Four studies so far have addressed the influence of solar activity on seagrass change over short-term time scales of decade(s). Global solar irradiance, together with tidal exposure, were found to be significantly and negatively correlated with seagrass biomass (Unsworth et al., 2012). In tropical seagrass meadows, several seagrass variables (canopy height, cover, and shoot density) have been observed to be negatively and unimodally correlated to solar sunspot activity (Marques et al., 2014; Alonso Aller et al., 2019). Solar sunspot activity results in increased solar irradiance (Willson & Hudson, 1991). Sunspot numbers have also been suggested as the main trigger of massive flowering events in *P. oceanica* meadows (Montefalcone et al., 2013)

Solar irradiance was suggested to have had an influence on the Iberian Peninsula climate and other regions in the Mediterranean over the late Holocene, through NAO (e.g. Versteegh et al., 2007; Nieto-Moreno et al., 2011; Morellón et al., 2012; Nieto-Moreno, 2012; Moffa-Sanchez et al., 2014; Ait Brahim et al., 2018; Moreno et al., 2018). Most studies assumed a linear relationship between solar forcing and NAO. The solar influence on NAO would be possible after feedback mechanisms amplifying solar variations. Solar variability could thus affect the oceanic and atmospheric circulation and, therefore, regional temperature and precipitation regimes (Thieblemont et al., 2015; Gray et al., 2017). The NAO accounts for the highest amount of variability of the recent climate in Europe (Hurrell, 2003), which may explain why most studies have only focused on the past role of this atmospheric pattern. However, other North Atlantic climate modes also influence the recent European climate variability. The East Atlantic Pattern (EA) and the Scandinavian pattern (SCA) modulate the location and strength of the NAO dipole (Trigo et al., 2008; Jerez & Trigo, 2013; Comas Bru & McDermott, 2014). The interactions between these climate modes are suggested to explain the spatiotemporal variability in the Iberian Peninsula climate over the last millennia (Sánchez-López et al., 2016) and even the annual variability of net biome productivity in Europe (Bastos et al., 2016). Therefore, relationships between these large-scale climatic modes and solar forcing are likely much complex than only a simple, linear correlation with NAO (e.g.

Georgieva et al., 2007). This would explain why NAO and TSI are not correlated in the PCA for large-scale climate variables (Fig. 2C). In fact, Sánchez-López et al. (2016) suggested that solar activity fluctuations were mainly reflected in the EA (negative/ positive phases associated with low/ high solar irradiance) and the interplays between the EA and NAO phases explained the overall climate conditions in the Iberian Peninsula better than NAO alone.

The diverse relationships between seagrass production and solar irradiance found in our study could be due to this interplay between solar forcing (mainly affecting EA phases) and NAO phases. Interplay that would be also reflected differently in each core because they cover different periods. Following this reasoning, a next step that could improve the models would be the inclusion of a covariate of interaction between solar irradiance and the NAO index. Our results highlight the fact that a proper understanding of the impact of solar activity remains still a challenge in paleoecological studies.

### Spatial differences of climate and local factors

Cores encompassing shorter periods and with higher accumulation rates were significantly less influenced by local factors but more influenced by climate. The model residuals in these sites were lower, although not significantly (Fig. S1). From these relationships, we could hypothesise that climate influence has been greater over recent periods. Another possibility would be that climate influence is underestimated at longer-time periods. The fact that models' residuals are negatively correlated with the influence of climate and positively with the time span covered by each core (Fig. S9) suggests that the influence of climate at longer time-scales may be underestimated in our models. This underestimation could be due to a problem of pairing time series because of higher age uncertainties in older samples. However, we cannot discard the role of the meadows' environmental settings. Higher sediment accumulation rates are likely due to higher terrestrial inputs, which, together with periodic upwellings, increase water turbidity, causing a decrease in light availability and hence in seagrass photosynthesis and growth (Ruiz Fernandez & Romero, 2001). Although other interacting factors associated to higher sedimentation rates would additionally explain seagrass decline, such as seagrass burial, increased nutrient concentrations and overgrow of other primary producers, as well as changes in sediment quality (Ruiz & Romero, 2003; Cabaço et al., 2008). All the negative impacts derived from the increased sedimentation rates could make the seagrass less resilient to climate changes, as discussed above. These less resilient meadows are mainly located in the western side of the mainland coast, in the Alboran Sea. This area is the westernmost geographical limit of *P. oceanica*. Meadows near this limit are spatially more fragmented and grow at narrower depth ranges (Mateo-Ramírez et al., 2016). Their reproductive success is suspected to be lower, with the first records of flowering events recorded recently (Urra et al., 2011). It seems that the constraints imposed by the environment in this area are not only limiting the seagrass growth but also making it less resilient to other disturbances. Conservation actions should be more robust in this area considering their natural constraints and that the coast along the Alboran sea has been massively urbanised. Anthropogenic impacts will likely increase further due to new urbanisation plans in natural coastal areas (Sánchez, 2020). These plans will probably be approved after the recent modification of the local government urbanistic law (Comunidad Autónoma de Andalucía, 2020).

## 5. CONCLUSIONS

This study illustrates the potentiality of fitting additive models to paleoecological data from seagrass meadows. It has allowed us to explain a moderate-to-high degree of deviance of long-term seagrass production in most of our study sites, and to identify its significant long-term drivers and their relationships. There was no single clear contributor to the long-term seagrass production. The environmental drivers considered had combined and varying influences in the study areas. We found a ubiquitous, although moderate, influence of fluvial discharges on long-term seagrass production. Terrestrial material had a negative influence in seagrass meadows receiving higher sediment loadings, which likely decreased underwater light availability. However, fluvial discharges had a positive effect in other meadows where sediment loadings were not that high, which could be due to terrestrial nutrients enhancing photosynthesis and not affecting light availability in a significant way. The global rise of temperatures due to anthropogenic activities had different impacts on seagrass production. In meadows that were also negatively affected by natural high fluvial loadings, global warming had a negative effect; while in meadows where underwater light was not limited, global warming had a positive effect, at least until very recently. This result suggests that seagrass meadows under compromised light availability were more sensitive to rises in seawater temperature. Other climate factors, such as the North Atlantic Oscillation mode, also had a significant influence, with overall higher seagrass production during negative NAO phases, humid periods likely increasing nutrient availability from upwelling waters and terrestrial discharges. The effect of solar activity on seagrass ecosystems, aside from its indirect influence through NAO, is not clarified by our results.

Even though our models could have underestimated the influence of climate in meadows where cores covered longer periods, due to higher age uncertainties in older samples, overall, our findings showed a significantly greater influence of large-scale climate in seagrass meadows receiving higher sediment loadings. This suggests that seagrass meadows naturally receiving higher fluvial discharges are less resilient to climate changes due to combined negative effects of local and climate factors. Therefore, local conservation and restoration plans would likely be more successful in seagrass meadows where underwater light is not impacted, because they seem to be more resilient to global warming. In contrast, seagrass meadows in which light availability is naturally lower seem less resilient and more sensitive to global warming and hence, conservation and restoration actions would have to be more robust and determined. These results suggest that *P. oceanica* meadows in its westernmost distributional limit are more affected by climate change so their decline could be faster if strong local conservation actions are not implemented.

## APPENDIX[4]

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[4] See supplementary materials in Appendix D.

# GENERAL DISCUSSION

Several studies talk about worldwide decline in seagrass cover, in particular during the last decades, due to changes caused or induced by anthropogenic changes (Orth et al., 2006a; Waycott et al., 2009; Short et al., 2011). However, other studies observed stable or even increasing trends in many meadows and, hence, deny the role of large-scale factors (González-Correa et al., 2007; Guillén et al., 2013). Whatever the reason(s), the observed decline is expected to continue, either because of global warming (Jordà et al., 2012) or local human threats that are expected to increase on the marine ecosystems (Halpern et al., 2019). The future decline is of particular concern for *P. oceanica*, having an overall rate of change of areal extent of -1.74% yr $^{-1}$ (Marbà et al., 2014), almost doubling the -0.9% yr $^{-1}$ estimated for seagrasses globally (Waycott et al., 2009), with reported losses even in protected areas (Marbà et al., 2002; Marbà & Duarte, 2010). Moreover, this seagrass has a very low recovery ability and is endemic of the Mediterranean, a hotspot area responding faster to global warming (Giorgi, 2006). Due to the accelerating worldwide decline of most seagrasses and the active discussion about the causes, this thesis addresses the long-term dynamics of seagrass meadows.

Paleoreconstructions using seagrass deposits have mainly focused on allogenic, externally controlled, processes. Specifically, these studies report on how the anthropogenic activities are recorded in seagrass sediments. Paleoecological studies that focused on how past environmental changes affected the seagrass ecosystem merely addressed the impact on the accumulation of organic carbon (see references in section 2.1 of the General Introduction). The view provided in this thesis is, in several aspects, broader than that of previous paleoreconstructions. First, several study sites were included, allowing a more regional perspective of the long-term changes. Second, to reveal the long-term dynamics of seagrass meadows at the community-level, autogenic and biotic ecological components of the ecosystem were addressed, aside from the organic matter accumulation aspect. For example, this thesis reconstructed the production of the seagrass, of other primary producers and even compositional changes of the photosynthetic community.

In marine ecosystems, local human stressors interact with climate change and their combined effects have been observed to be context-dependent and vary between ecosystems, although our understanding is still limited (Gissi et al., 2021). Identifying the causes and their relative importance could help to design more efficient management plans. However, the plausible influence of large-scale climate factors has been widely ignored in seagrass paleostudies so far. The long-term paleoecological data of this thesis could help to elucidate the role of local and global factors in the current declining trend of many seagrass meadows.

The results obtained provide valuable information about the long-term seagrass ecosystem dynamics in the Western Mediterranean, which certainly helps to frame current seagrass status, clarify the plausible causes of long-term change as well as their role, and even anticipate future ecological changes.

# 1. UNVEILING LONG-TERM PROCESSES RECORDED IN SEAGRASS SEDIMENTS

## 1.1. Biotic autogenic processes of seagrass meadows

A first and keystone step of most paleoecological studies is the interpretation of the information preserved in the sediments through the use of proxies. Given the novelty of the paleoreconstructions using seagrass sediments, many proxies and techniques are still to be properly assessed. In **chapters 1, 2** and **3**, several new proxies and a technique were tested to identify processes related with different biotic components of seagrass meadows, focusing on the principal photosynthetic producers: the seagrass itself, micro- and macroalgae (McRoy & McMillan, 1977). The different proxies used in **chapters 1-3** contributed to understand the long-term dynamics of the whole primary producer's community (Fig. 1)

In **chapter 1**, biogeochemical proxies from seagrass debris were found to be likely related to seagrass processes. The stable carbon isotope signature of the sheath remains from past seagrass leaves ($\delta^{13}C_{SHEATH}$) was expected to be related to seagrass production, as previous field and lab studies found positive correlations between $\delta^{13}C$ of the sheaths, light availability, and seagrass photosynthesis and productivity (Grice et al., 1996; Hemminga & Mateo, 1996; Mateo et al., 2010; Hu et al., 2012). As expected, paleodata of $\delta^{13}C_{SHEATH}$ seemed indicative of past seagrass productivity, given its covariation with the accumulation rate of carbonates. Carbonates in the seagrass meadows are mostly of biogenic origin. The biogenic calcification is facilitated by the elevated pH derived from higher seagrass photosynthesis (Semesi et al., 2009; Hendriks et al., 2014; Guilini et al., 2017). Moreover, pH fluctuations induced by *P. oceanica* metabolism have been observed to protect and confer resistance to its epibionts to the ocean acidification (Ramajo et al., 2019). The covariation of $\delta^{13}C_{SHEATH}$ and carbonates accumulation could be a reliable proxy of seagrass productivity in other study sites, provided, of course, that carbonates are not sourced from the terrestrial catchment, and hence, the lithogenic source can be discarded (Gaglianone et al., 2017).

In **chapter 1**, the PCA performed on the biogeochemical proxies analyzed in the Portlligat meadow also revealed another principal component related to production, besides the seagrass productivity. This principal component showed high loadings for organic matter accumulation. Organic matter (OM) is usually considered a proxy of the whole ecosystem primary production, although it can be affected by post-deposition and later diagenesis (Pedersen & Calvert, 1990; Rullkötter, 2006). However, in seagrass meadows, where sediments rapidly achieve anoxic conditions (Marbà et al., 2006; Mateo et al., 2006), OM preservation is highly enhanced. Moreover, the fact that systematic downcore decreases in OM content are not observed in Portlligat nor in other seagrass meadows (Piñeiro-Juncal et al., submitted) discards significant post-depositional mineralization and points to variations in supply as the main driver (Rullkötter, 2006).

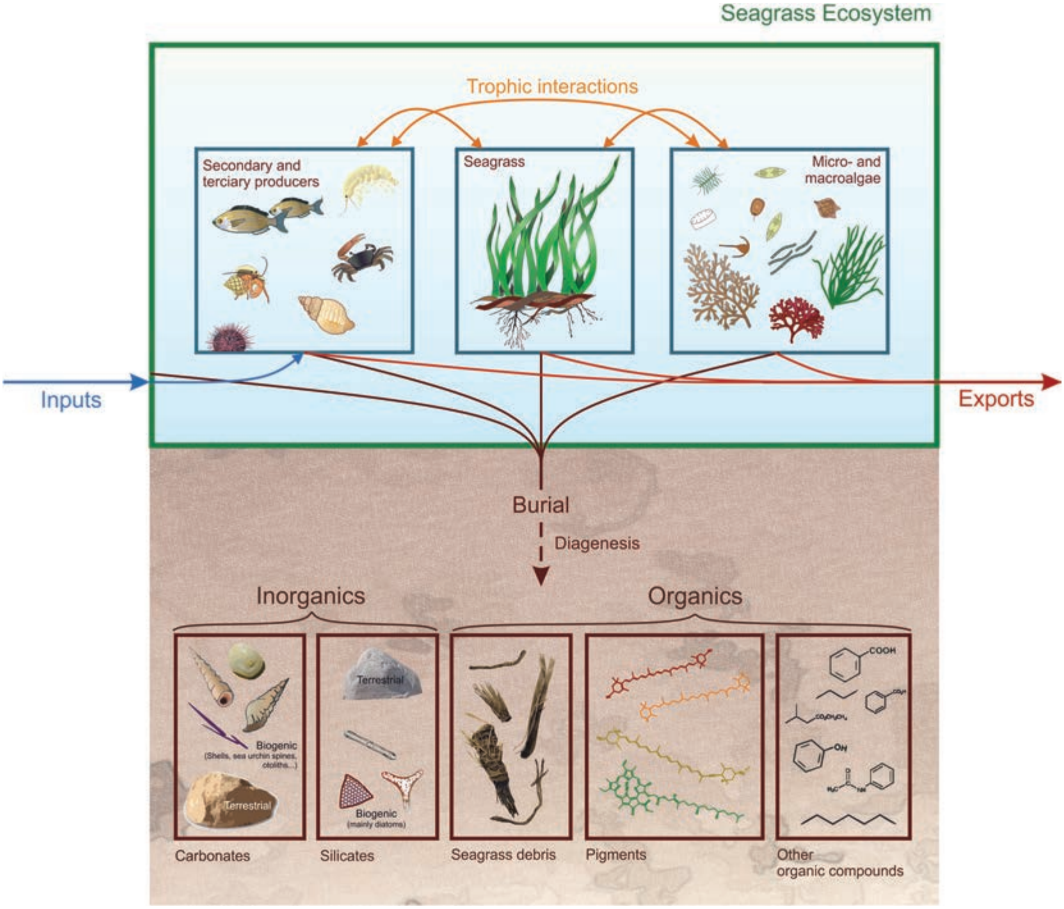


**Figure 1.** Diagram illustrating the main biotic components of the seagrass ecosystem, the fluxes between biotic components (arrows) with the main sedimentary components, and the type of materials sequestered in the deposits below the seagrass meadows. Most of the sedimentary components illustrated here were used as proxies in this thesis.

Therefore, it seems there is an unalignment between the ecosystem and the seagrass primary production, which is not only evident in the results obtained for the Portlligat meadow (**chapter 1**) but also those obtained for the Andalusian meadows (**chapter 3**). Total OM and polysaccharides content (carbohydrates present in any primary producer and are easily degraded) were found to covary, likely associated with the primary production of the whole community. However, another synthetic variable related to the abundance of seagrass macrodebris and molecular composition characteristic of the seagrass organic matter - aromatics, phenols, carbohydrates and lipids- and likely more representative of the seagrass production was found. This unalignment proofs that the seagrass does not drive the ecosystem production alone, with other producers having a significant contribution too. Other primary producers, such as epiphytes, phytoplankton, micro-phytobenthos and macroalgae, can contribute up to 60% of the total seagrass ecosystem production (Borowitzka et al., 2006; Mateo et al., 2006). The unalignment is also proof of unparalleled production dynamics between the seagrass and other primary producers. The most simple explanation is that drivers behind seagrass and algal production are different and not necessarily correlated; which makes sense considering the different ecological requirements of the seagrass and the algae (Hemminga & Duarte, 2000).

However, the lack of correlation between the production of the ecosystem and that of the seagrass was not evident in the Cabrera meadows. Cores from meadows around the island showed an OM content (the whole ecosystem production) covarying with compounds typically present in seagrass debris. In other words, temporal changes of the primary production for all producers were more or less parallel, and so they combined into the same synthetic variable. This could indicate that all the photosynthetic components are limited and driven by the same factor in Cabrera, while along the mainland coast, there seem to be several drivers with differential influence on the primary producers. Waters around the Cabrera island are oligotrophic (Ballesteros & Zabala, 1993), so nutrient availability is the most plausible factor limiting the growth of all the producers there. In oligotrophic waters where nutrients are the only limiting factor, nutrient additions result in positive responses of seagrass growth and physiology (Romero et al., 2006). This is what the results in **chapter 3** indicate because the synthetic variable related with the ecosystem and seagrass production includes $\delta^{15}N$, which can be a proxy of increased inputs of inorganic nitrogen (Talbot, 2001). In oligotrophic environments, such as the Cabrera waters, the $\delta^{15}N$ of sinking OM (and of N in sediments) is expected to match that of the nitrate supply because the nitrate pool is completely consumed in oligotrophic waters (Altabet & Francois, 1994).

The proportions of debris from different seagrass organs (sheaths, rhizomes and roots) merged into a synthetic variable revealing an aboveground/belowground organ ratio (AG:BG). This allometric ratio varies in seagrasses in response to changes in nutrient availability and light, although the direction of change might be different depending on the seagrass conditions prior to a disturbance (Lee et al., 2007; McGlathery, 2008 and references therein; Han et al., 2016; Barry et al., 2017). For example, investment in belowground biomass is usually lower if the seagrass can obtain nutrients from the water column through the leaves, causing higher AG:BG values. Nutrients as a main driver of this ratio was supported by the findings in **chapter 1**, considering the positive covariation of the aboveground biomass with the N content of sheath debris. Moreover, the seagrass belowground biomass has a lower turnover rate after disturbance than aboveground biomass. This means that high values of this ratio could also reflect decreased belowground biomass due to long-term impacts (Carlo & Kenworthy, 2008; Vonk et al., 2015). Since the biogeochemical proxies from seagrass debris were only studied in one core (sampled in the Portlligat meadow), a broader spatial study would be needed to confirm if the factor driving this proxy remains the same in other meadows.

In **chapter 2** the focus was set on the whole community of primary producers. Sedimentary pigments were used to assess changes in the composition and production of the photosynthetic community. One of the main concerns when using sedimentary pigments is their preservation (Leavitt & Hodgson, 2001). There was, hence, the need to prove that the observed temporal trends were not affected by post-depositional changes in the preservation of pigments. We found that diadinoxanthin (related to dinoflagellates) was the only pigment that may have been affected by degradation because it showed almost exponential trends with age in all cores. Nevertheless, the preservation issue was finally discarded because dinoflagellate cysts, resistant microfossils which are well preserved in sediments (Versteegh & Blokker, 2004), showed the same trends as the pigment. Therefore, the observed sedimentary changes were more likely a reflection of actual changes in dinoflagellates biomass. The overall results of the study on pigments revealed that communities were mainly composed of diatoms, dinoflagellates, cyanobacteria, red algae and seagrass. The ability to obtain paleodata from other biotic components than the seagrass is key because seagrass ecosystems might be impacted through effects on other components, such as changes in the associated algal (micro- and macro-) communities. Nutrient supply is usually considered the main factor that can disrupt the balance between seagrass and algae, changing the community structure and, hence, its functions (Burkholder et al., 2007; Hauxwell & Valiela, 2007; McGlathery, 2008). The results obtained with pigments revealed that the long-term balance between seagrass and algae was disrupted not only by changes in nutrient supply (related to local spatial differences of terrestrial discharges) but mainly by energy influx. The major temporal change in the photosynthetic community was driven by changes in irradiance and heat over the last century. Changes in light and temperature reaching the surface seawaters can affect the structure of the photosynthetic community because species have different tolerances and ability to adapt (e.g. Hallegraeff, 2010). Although their effect can also be indirect, through changes in water chemistry ($CO_2$, pH) or physically driven changes that may affect nutrient availability (surface water stratification, sea level, wind and upwelling intensity; Harley et al., 2006). Global warming largely affects this energy influx into the water column, so pigments in seagrass sediments can help us to understand and predict the photosynthetic community responses to these recent abiotic disturbances. Further work, using pigments analysis, may help to check the dynamics of past communities of photosynthetic producers along the mainland, in meadows where waters are more light-limited and nutrient-richer than those around Cabrera Island.

The paleoecological potential of Fourier-transformed Infrared spectroscopy (FTIR) technique was evaluated in **chapter 3**. It proved to be a very valuable tool to identify components of biological origin since it allowed a general overview of the different organic compounds preserved in the deposits. All processes identified were somehow related to the production of different biotic components: the balance between different sources of organic matter, the whole ecosystem production and the seagrass production. The first principal component in both study areas, Andalusia and Cabrera, explained between 65 to 70% of the total variability and were likely related to the balance between different primary producers. This means that the bulk OM preserved in the deposits is a combination of different organic compounds, which highly varied between meadows, as was also previously reported for *P. oceanica* meadows (Papadimitriou et al., 2005). The OM compounds involved in this balance provide information on the sedimentary conditions and the OM sources (primary producers' composition and terrestrial organic inputs), not always independent from each other. Aromatics, phenolics, polysaccharides and linings were likely related to meadows were seagrass was the main producer. These OM compounds can be seagrass-derived and have a high preservation potential because of their recalcitrant nature (Kaal et al., 2016). In contrast, meadows with a higher amount of aliphatics (mainly lipids and nitrogen-containing compounds) in the sediments were more likely indicative of higher algal biomass relative to seagrass. Aliphatics are usually labile and easily decomposed in anaerobic marine sediments (Tremblay et al., 2011); therefore, there must be processes enhancing their preservation. In Andalusia, meadows with higher aliphatic content in their sediments were also those with higher terrestrial inputs (BA, ME, and CA). The preservation of algal derived compounds was most likely favoured by the terrestrial influx, either because of a higher proportion of finer sediments from the terrestrial catchments or due to higher accumulation rates. Previous studies did also observe a high accumulation (up to 72%) of sestonic particles in *P. oceanica* meadows (Gacia et al., 2002) as well as high preservation of OM from seston in its sediments (Mazarrasa et al., 2017a).

This pattern of aromatics vs aliphatics, being indicative of seagrass vs algal production, is observed along the Andalusian coast. The balance was different and the same compounds were indicative of different conditions in the bays sampled in the Cabrera Island. Aliphatics were especially abundant in SM Bay, a nutrient-limited meadow, where algal biomass is not supposed to be higher than that of the seagrass, given the oligotrophic waters. The accumulation of aliphatics was initially counterintuitive. The plausible reasons are, first, that meadows in the Cabrera island are located in enclosed bays while those along the mainland are more exposed meadows. The longer water residence time of the bays could favour higher sestonic inputs; and second, the usual groups of algal producers growing together with the seagrass in nutrient-limited waters are epiphytes and macroalgae (Borowitzka et al., 2006; Burkholder et al., 2007). Epiphytes grow over the seagrass, so they are close to the substrate, and its deposition and burial can be faster than algal producers living in the water column. Therefore, they could be less degraded before deposition. Overall, aliphatics in seagrass sediments can be related to different environments that either favour algal growth (terrestrial and nutrient discharges) or its higher deposition (enclosed bays with lower water turbulence and higher residence times) or even both. Both environments derive in sediment conditions (high accretion rates and/or finer sediments) that can physically protect aliphatics so that these labile molecules could largely escape the early diagenesis and accumulate (Hedges et al., 2001; Serrano et al., 2020).

The proxies defining the synthetic variables related to seagrass production differed in each study area, although there were few proxies in common such as some organic compounds from seagrass tissues. The same ecological function, the seagrass production, can be recorded in the deposits through different proxies because seagrass production can be affected by multiple factors and their interactions (Lee et al., 2007; Ontoria et al., 2019b). For example, nutrient-limited meadows can have different limiting nutrients, whose availability depends on local nutrient regimes (Alcoverro et al., 1997), which can be ultimately controlled by very diverse indirect factors. This emphasizes the need for using a multiproxy approach for a complete and reliable reconstruction of the seagrass production at every study area where a paleoapproach is planned.

### 1.2. The long-term role of herbivores: preliminary results and potential in future studies

The top-down effect of herbivores significantly regulates the dynamics of seagrass meadows, a regulation that can largely vary over time (Heck & Valentine, 2006; Valentine & Duffy, 2006; Whalen et al., 2013; Steele et al., 2014; Bakker et al., 2016). Herbivores can constrain the abundance and composition of the primary producers in the meadows which influences the functioning of the ecosystem (Tomas et al., 2005b; Prado et al., 2007a, 2007b; Vergés et al., 2007; Duffy et al., 2015; Bakker et al., 2016). In temperate seagrass meadows, herbivores can be classified into mesograzers (amphipods, isopods, and gastropods) and macroherbivores (sea urchins and fish). While macroherbivores have a more significant and direct impact in the decline of seagrass abundance (Prado et al., 2007b), mesograzers can have indirect positive effects on seagrass abundance, because they mainly graze leaf epiphytes, which reduces their shading effect (Duffy et al., 2001; Borowitzka et al., 2006). The herbivory pressure on seagrass meadows will likely be altered in the future with the expected changes derived from global change (e.g. higher temperatures, lower pH), as well as the intensification of local stressors (e.g. eutrophication). These disturbances have been observed to alter the consumption rates of seagrasses by modifying leaf C:N ratio or phenolic content, i.e. leaf palatability, which may ultimately enhance seagrass grazing (Heck & Valentine, 2006; Arnold et al., 2012; Steele & Valentine, 2015; Jiménez-Ramos et al., 2017). However, seagrass-herbivore interactions are complicated and more research is needed to elucidate the mechanisms behind these interactions (Heck & Valentine, 2006; Marco-Méndez et al., 2015, 2016). To predict future ecosystemic changes reliably at the community level, it is of great importance to comprehend how species interactions and the community composition can be modified. The role of herbivory in the seagrass community and how the performance of grazers changes under global and local disturbances could be better understood if assessed over long time periods.

After fish die, their otoliths, calcified structures that are bones from the inner ears, can accumulate in marine sediments. Otolith assemblages from deep marine sediments have been used to reconstruct past fish communities and abundance even over the last two millennia (Lin et al., 2017; Jones & Checkley, 2019). Although the presence of otoliths has not been assessed in seagrass sediments, they are likely accumulated and preserved in these deposits due to the high abundance of fish in seagrass meadows (Gillanders, 2006) and the overall well preservation of otoliths in sediments of shallow waters (Lin et al., 2017). Fish otoliths would potentially be further preserved in seagrass deposits considering the alkaline conditions in seagrass beds due to their intense photosynthetic activity and also within their sediments (Morse et al., 1987; Mazarrasa et al., 2015; James et al., 2020). Two regular echinoids are found in *P. oceanica* meadows: *Sphaerechinus granularis*, and *Paracentrotus lividus*. Low densities of *S. granularis* can be observed in *P. oceanica* meadows while *P. lividus* is quite common, being one of the main consumers of the plant (Tomas et al., 2005b; Heck & Valentine, 2006; Prado et al., 2007b). The benthic sea urchins tend to disarticulate, and parts of their skeletons (spines and other fragments) found in the sediments attest for their presence. The past presence of sea urchins and even changes in their population density could be assessed through the study of their fragments along sediment cores (Kier, 1977; Nebelsick, 1992; Greenstein, 1993). Within the frame of this thesis, preliminary results of sea urchin spines over the core AG were obtained. These results revealed long-term abrupt changes in the sea-urchin presence, which were significantly and negatively associated with the seagrass macro-debris (GAM model, adjusted $R^2 = 0.36$, $p < 0.001$), so they could have partially influenced the dynamics of the seagrass community at site AG (Fig. 2).

There are some mesograzers, such as gastropods (e.g. *Bittium reticulatum* and *Jujubinus striatus* in *P. oceanica* meadows; Gacia et al., 2009) that also leave proofs of their existence in the sedimentary records. Future studies could evaluate the long-term influence of these herbivores through the calcareous shells left by these organisms. A paleoecological perspective could help to understand further the impact of herbivory in seagrass communities, as well as how and why the feeding patterns and performance of the grazers changed under past global and local disturbances.

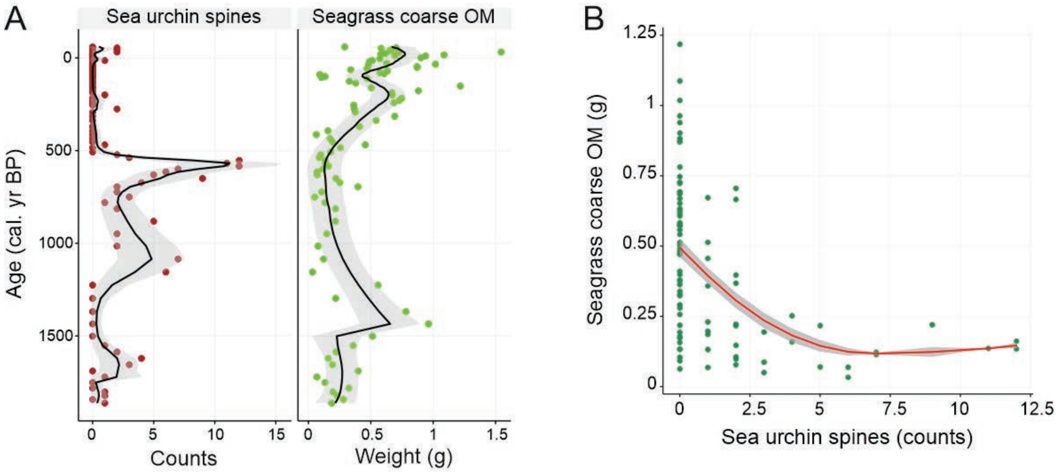


**Figure 2**. A) Temporal records of sea urchin spines and coarse seagrass debris along the core extracted in Aguamarga location (AG). Black solid lines indicate the fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. B) GAM-modelled relationship between sea urchin spines and coarse seagrass debris ($R^2$ adjusted = 0.36). Variance heterogeneity of sea urchin spines for seagrass debris was included in the model. The solid red line indicates the fitted smooth functions of seagrass and grey shaded regions are 95% point-wise confidence intervals. GAMs trends are significant ($p < 0.05$).

# 2. SEAGRASS LONG-TERM ECOSYSTEM DYNAMICS AND SOURCES OF VARIABILITY

## 2.1. Long-term temporal dynamics of seagrass production

### A naturally dynamic system and their recent decrease

In **chapter 3**, a relationship between current values of mean shoot densities and the mean values of the corresponding scores for the synthetic variables related to seagrass production was revealed. The mean values of the scores were calculated with values within the same time period as the current mean shoot densities. This correlation could be used as a calibration function to reconstruct shoot densities from the scores of the synthetic variables, reconstructing absolute values of shoot density along the last centuries and millennia (Fig. 3). We should keep in mind that the number of scores values that were used to calculate the mean between AD 2000 and 2018 were quite scarce, sometimes even just one. Therefore, the calibration function is not accurate, and the reconstructed absolute values of shoot densities should be interpreted with caution.

Throughout the temporal series of shoot density, periods with a significant change mostly occurred over the last 150 years (Fig. 3). More specifically, the main common trend is the decrease of the long-term seagrass production since ~1850 AD along the mainland coast. In the paleoreconstruction of Portlligat (**chapter 1**), the results also revealed a period of low and decreasing ecosystem and seagrass production over the last two centuries.

However, the results reveal increasing or stable trends in meadows of the Cabrera Island for the same time period. Seagrass dynamics have been mostly studied up until the 1850s, through the use of reconstructive techniques (lepidochronology and the intermodal length method (e.g., Marbà & Duarte, 1997; Marbà et al., 2002; Peirano, 2002; Mayot et al., 2005; González-Correa et al., 2007) or direct observations (e.g. Marbà et al., 1996b, 2014; Díaz-Almela et al., 2009; Peirano et al., 2011; Terrados & Medina-Pons, 2011; Guillén et al., 2013). The main global temporal trend observed for seagrasses is a decrease of its areal extension at a median rate of ~1% yr-1 and thinning of the remaining underwater vegetation since AD 1850, accelerating to a 5% yr-1 after 1980 (Waycott et al., 2009). While most studies conclude that the seagrass decline is globally widespread, they also recognize that there is substantial variation in seagrass trends at local and regional scales (Marbà et al., 2005; Boudouresque et al., 2009a; Waycott et al., 2009; Telesca et al., 2015). A spatial variation that is also observed between the two main regions of study in this thesis, Andalusia and Cabrera.

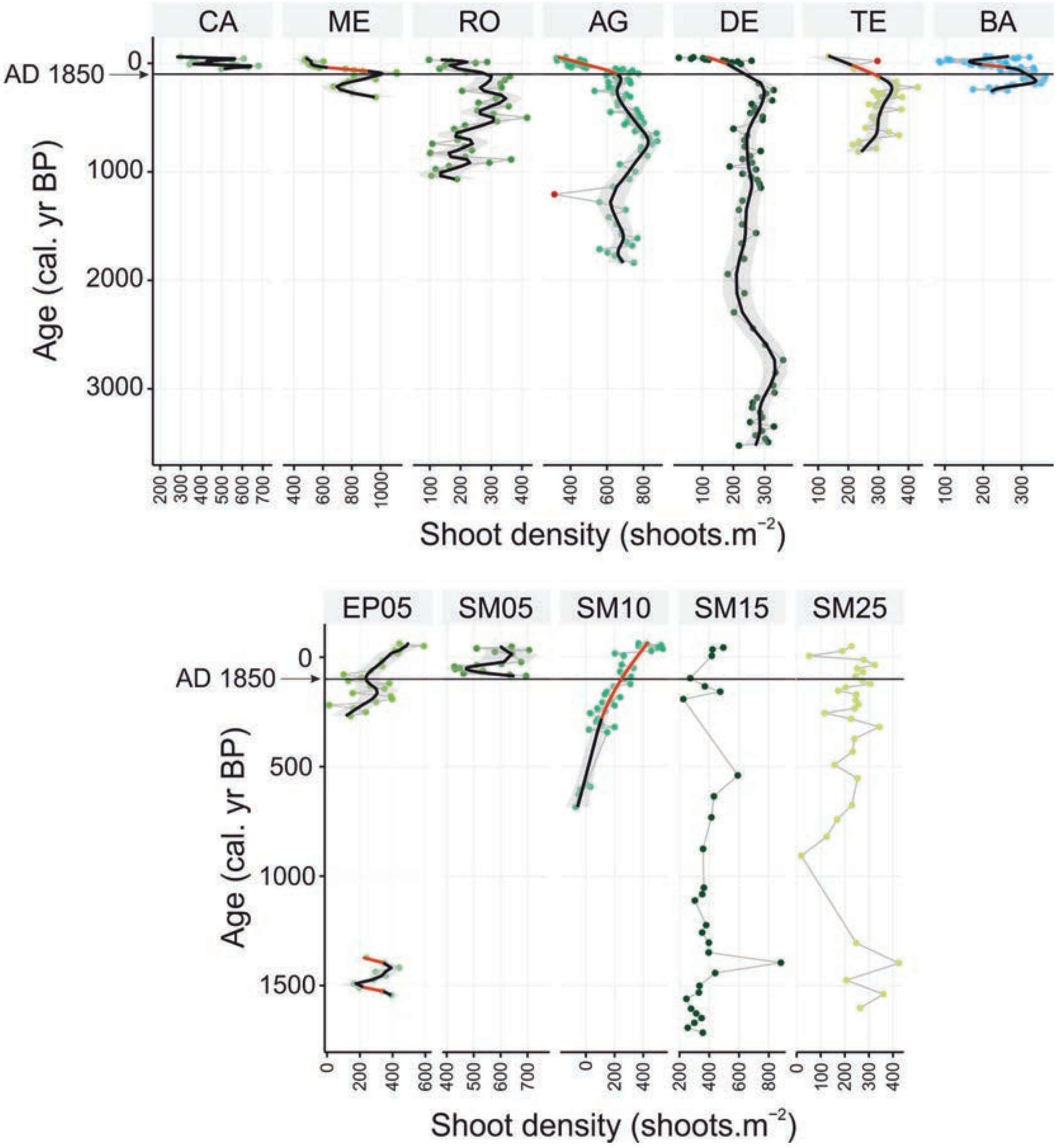


**Figure 3.** Temporal records of reconstructed shoot density for every core along the coast of Andalusia and from the Cabrera Island. Abbreviations above records (CA, ME…) correspond to the code of the core. Black solid lines indicate the fitted smooth functions of time (GAM models, formula=$y \sim s(x)$) and grey shaded regions are 95% point-wise confidence intervals. Red solid lines show periods of significant change (either increases or decreases), significant means that the first derivative of the fitted trend from the GAM model is different from zero. Only GAMs with significant ($p < 0.05$) trends are shown. Red points were considered outliers and not included in GAM models.

The long-term seagrass declining trends appearing only along the mainland coast since AD 1850 could be attributed to the conjunction of several factors: (1) synergies between global and local anthropogenic impacts, more intense and frequent impacts along the mainland due to a considerable higher population, growing since the early 20th century compared to the tiny and oscillating population in Cabrera; (2) the closeness of the Andalusian meadows to the edge of the *P. oceanica* biogeographical range (North-western Alboran Sea), closer to its physiological thresholds, which may make the seagrass populations there more vulnerable to perturbances (Fraser et al., 2014; Tuya et al., 2018); and (3) a plausible more intense long-term seawater warming in the Alboran Sea and higher water temperature variability (Shaltout & Omstedt, 2014), despite its lower average sea surface temperature, pointing to temperature variations as drivers of seagrass change rather than absolute values.

To compare recent estimates of seagrass change with the long-term ones estimated in this thesis, the absolute rate of change of the reconstructed shoot density (shoots $m^{-2}$ $yr^{-1}$) was calculated for periods of 50 years since 1700 as follows:

$$\text{ABS} = (N_t - N_0) / t$$

where $N_t$ is shoot density (shoots $m^{-2}$) at the end of the period, $N_0$ the shoot density at the beginning of the period, and t the observation period (~50 yr). The long-term rates of change (Fig. 4) confirmed what we could observe in the temporal trends: negative rates of change started in ~1800-1850 and continued to the present in most of the seagrass meadows along the Andalusian coast. There is also a slight trend of more negative rates of change towards present in the mainland meadows located nearer the western side (CA, ME, and RO). The rates of change in the Cabrera Island were quite oscillating over the last centuries and did not reveal a clear trend in any core. The lowest absolute rates of shoot density change over the last century are close to -5 shoots $m^{-2}$ $yr^{-1}$, quite lower compared to the overall estimate at -27.5 +/- 9.07 shoots $m^{-2}$ $yr^{-1}$ over the last decades (Marbà et al., 2014). This could indicate that the decline of seagrass abundance has greatly accelerated over the last decades. However, our estimate is probably not very precise, because the calibration function used had wide error bands (Fig S6). Therefore, the acceleration of the decrease over the last decades might not have been as conspicuous as it initially seems.

Overall, the reconstructed seagrass production reveals naturally oscillating dynamics over centuries and millennia in every meadow (Fig. 3). These long-term oscillating dynamics seem to be a natural characteristic of the seagrass meadows in response to environmental variability, as these dynamics were already present at time periods with none or low human impact.

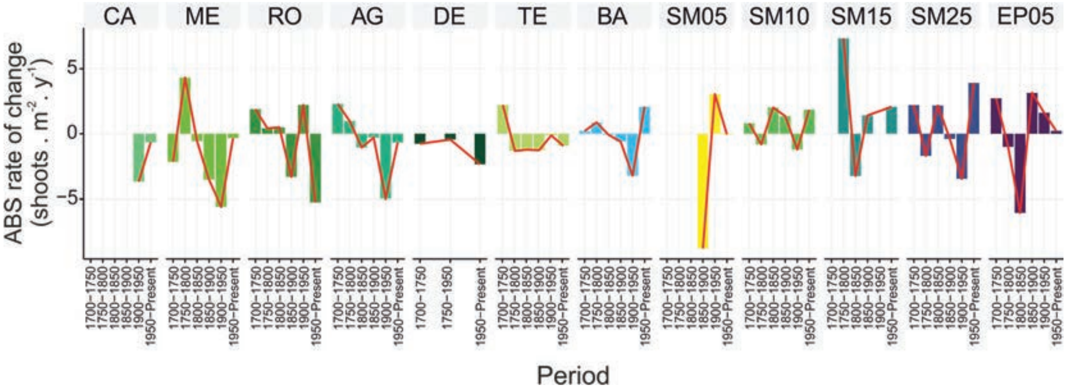


**Figure 4.** Absolute rates of change of the reconstructed shoot density calculated for periods of ~50 years since 1700 in every study site.

Interannual oscillatory dynamics of several parameters of the seagrass (leaf production, vertical rhizome growth, shoot density, seagrass cover) and of the other organisms inhabiting the meadows (leaf epiphytes cover, grazers' activity) were also described at recent decadal scales (e.g. Marbà & Duarte, 1997; Peirano et al., 2011; Alonso Aller et al., 2019). However, in **chapter 3**, results revealed that the degree of dynamism of seagrass production, i.e. its temporal variability, varied among locations. The main pattern observed was a trade-off between stability and production: the more productive a meadow is, the more oscillating are its long-term dynamics (Fig 6 of **chapter 3**). This variability over time is usually related to the resilience of the ecosystem. The resilience here, specifically, the ecosystem resilience, is defined as the ability of the ecosystem to absorb perturbations and reorganize while undergoing change so that it still retains essentially the same fundamental structure, functioning and feedbacks without shifting from one state to another (Holling, 1973; Walker et al., 2004). Ecosystem resilience encompasses both resistance, the ability to persist during stress, and recovery after perturbations cease (Unsworth et al., 2015). Increased variance over time can be indicative of slower recovery rates from perturbations, and hence, lower resilience (Scheffer et al., 2012, 2015). Therefore, higher productive meadows showing higher variability of its production over time likely have lower resilience and could tip more easily into an alternate state if disturbed.

The mentioned long-term trade-off could have profound implications regarding ecosystem management aiming to increase seagrass resilience. The main traditional metrics used in monitoring programs focus on simple attributes such as the areal cover, seagrass abundance at individual or population levels, shoot/leaf biomass or production and shoot density or carbon accumulation in soils (Kirkman, 1996; Short & Duarte, 2001; Roca et al., 2016). Even though the resilience of an ecosystem is considered more important than its current conditions (Holling & Gunderson, 2002) and that ecological stability and resilience are very influential concepts in ecology, they are rarely used in management or restoration plans.

More recently, several studies have addressed the importance of aiming for ecosystem resilience to halt global seagrass degradation (Unsworth et al., 2015). The inclusion of the temporal variability of seagrass indicators over long-term periods could help managers to more reliably assess the ecosystem status or the adequacy of a specific restoration project (Moreno Mateos et al., 2020). Considering the trade-off between seagrass production and its stability, a meadow with low-medium levels of production could be considered healthy if that production deviates little from its equilibrium over long-term periods, having faster recovery rates after perturbations.

### 2.2. Dynamics of long-term resilience of seagrass

The dynamics of resilience in seagrass meadows are not well understood due in part to the scarcity of long-term information (Duarte, 2002). The ecosystem resilience can be directly measured only with long time series of the variables describing the ecosystem (Thrush et al., 2009), as this data is available in this thesis I will try to better characterize the ecological resilience of seagrass meadows by using stability landscapes. A stability landscape is a multidimensional state space representing all possible states of a system. The ecosystem is viewed as a ball within these landscapes of stability, where there are basins of attraction (valleys or domains), each corresponding to a stable state in which the ecosystem tends to remain. The state space is dynamic, which means that the topography is continuously fluctuating, being mainly influenced by external factors (Walker et al., 2004). Wider and deeper basins of attraction, also usually with steeper slopes (representing the recovery rates) have higher ecological resilience, and require larger inputs of energy (i.e. a larger perturbation) to move the system out of the basin of attraction (Fig. 5A). Smaller and shallower basins of attraction usually have less steep slopes (Fig. 5A), which means that the recovery rate upon small perturbations is slower (Scheffer, 2009, 2012; Clements & Ozgul, 2018).

The stability landscape can be estimated through the probability density distribution of the state of the system (Scheffer et al., 2012, 2015). In our seagrass meadows, the system state variable that we are initially using is the reconstructed seagrass shoot density. The estimated stability landscapes are in Fig. 5B. Meadows with deeper basins seem to be closer to the eastern side of the Andalusian coast (RO, BA, DE and TE) or at deeper areas in the Cabrera Island (SM15, SM25). As expected, the most productive meadows, also the ones with higher variability over time as mentioned before, have shallower basins of attraction, a sign of lower resilience (CA, ME, and AG in Andalusia, as well as SM05, SM10, and EP05 in Cabrera). The higher variability of these meadows and its lower resilience indicate that these ecosystems could then more easily tip into an alternative state (Scheffer et al., 2015), to a regressed meadow

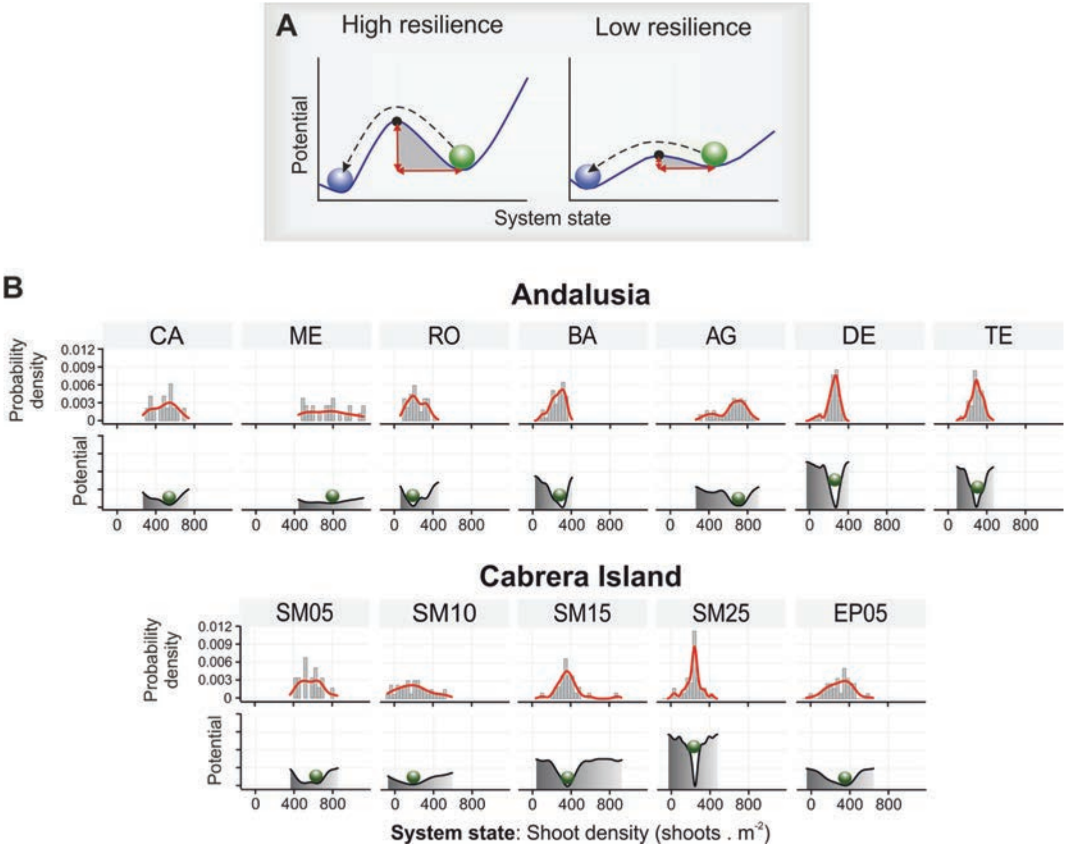


**Figure 5.** A) Representation of stable states, stability and resilience using stability landscapes. The state of the system corresponds to the position of the ball on the landscape (the solid purple line). Red and black solid arrows show the size of the basin of attraction. Larger and deeper basins correspond to systems with higher resilience. The green ball represents the healthy state of the ecosystem. If the system surpasses a tipping point (the solid black dot), it arrives to a degraded stable state (position of the blue ball). Figure adapted from Clements & Ozgul (2018). B) The probability distribution of states (shown in the above panel of each core) can be used to infer the shape of the stability landscapes (shown in the graph below each core) as stated by Scheffer et al. (2015).

or even they could be colonized by species with lower ecosystem engineering potential such as the seagrass *C. nodosa* or algal species of the genus *Caulerpa*. The substitution by smaller seagrass or invasive algal species would be a profound phase shift because their ecosystem services cannot be compared with those provided by *P. oceanica* (Montefalcone et al., 2011, 2015). The replacement of *P. oceanica* by *C. nodosa* has been already reported at some regions of the Mediterranean Sea (Montefalcone et al., 2007; Burgos et al., 2017). Interestingly, the only *C. nodosa* meadow in this thesis, BA, has a basin of attraction similar to other *P. oceanica* meadows (TE) and even deeper than other *P. oceanica* meadows (CA, ME, RO and AG). Garrido et al. (2013) also found a high degree of stability for *C. nodosa* in a Mediterranean lagoon, likely due to its high capacity of recovery based on its fast growth and colonization (Kilminster et al., 2015; O'Brien et al., 2018b).

There are meadows with multimodality of the frequency distribution, i.e. with two basins of attraction, such as AG, RO, and more slightly, DE and BA. The explanation to this could be that these sites have recently been exposed to external forcings because when an ecosystem is approaching a change of state due to exposure to perturbations, there can be changes in its stability landscape so that alternative basins of attraction (states) emerge (Scheffer et al., 2012).

We could go even further and reconstruct a two-dimensional stability landscape using the probability density distribution of two state variables: the PC related to seagrass production and the PC related to terrestrial inputs (Fig. 6). Two main patterns can be differentiated in Fig. 6. The first one reveals that in areas where terrestrial inputs are lower seagrasses display deeper valleys, which translates into a greater resilience than in areas where terrestrial inputs are higher. These results highlight the key role that the environmental conditions (current and preceding) have on seagrass resilience. Seagrasses located in areas naturally receiving higher terrestrial material and hence living closer to minimum light requirements, seem more vulnerable to other stressors, a result that was clearly observed in **chapter 4** through the use of GAMs models (see section 3). The importance of local and regional environmental conditions, especially of water turbidity and light availability, to the resilience of seagrasses within species was already acknowledged by Unsworth et al. (2015) and O'Brien et al. (2018a). The second pattern observed concerns seagrass production. As previously mentioned, the general pattern is that meadows with higher production also have shallower basins and lower resilience. In this 2D-stability landscape we can also see that if seagrass production is reduced, meadows under a higher arrival of terrestrial material (ME) will change more easily into a degraded state in which *P. oceanica* is substituted by *C. nodosa* (BA). Therefore, seagrass meadows receiving higher amounts of terrestrial material over the long-term are more likely to be under reduced levels of resilience. These meadows will be in a more vulnerable state against other impacts such as future climate change and local anthropogenic disturbances. The seagrass ecosystem resilience does also depend on the abiotic or biotic feedback loops that prevent or facilitate state shifts following disturbances, and these feedbacks are strongly site-specific and depend on the seagrass morphological and life-history traits and the prevailing environmental conditions (Maxwell et al., 2016). For example, the main studied feedback is a positive feedback based on the sediment trapping capacity of seagrasses, which improves water quality and favours seagrass growth and depends on the seagrass density and spatial cover of the meadow. Seagrass meadows in the western area of the Andalusian coast are patchier, shallower, covering less area (CAGPDS, 2018).

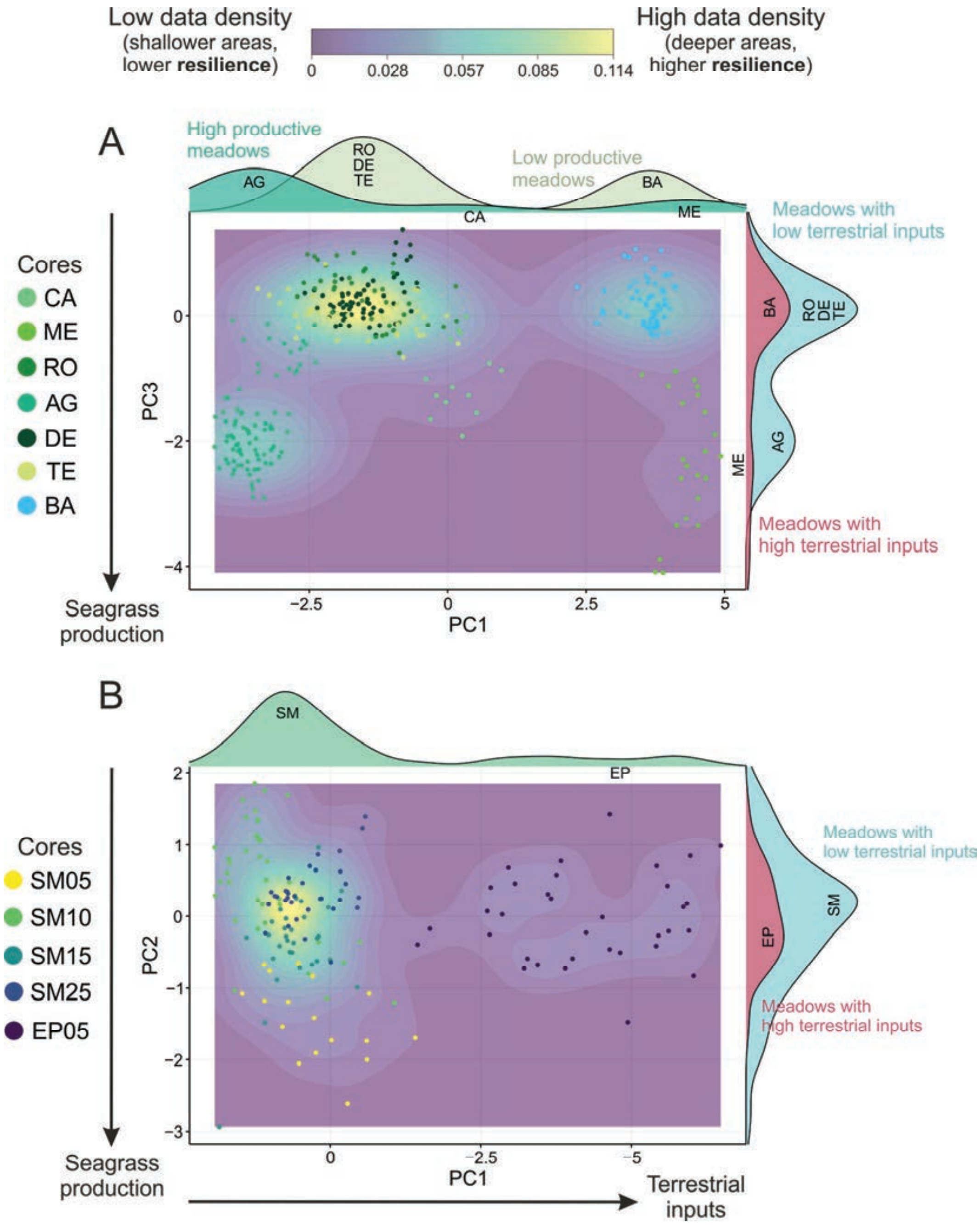


**Figure 6.** 2D kernel density contour plots of PC scores related with terrestrial inputs into the seagrass meadow (x axis) and with seagrass production (y axis) for A) Andalusian cores and B) Cabrera Island cores. Data density was calculated with a kernel density estimate. Contoured colours indicate the data density. These 2D density plots can serve as 2D stability landscapes, with yellow-green colours representing deeper basins of attraction while purple colours correspond to shallower areas. Marginal charts at the top and the right show the 1D stability landscape, i.e. the distribution of each variable using 1D density profiles, also differencing between groups of meadows. Note that all the study sites correspond to *P. oceanica* meadows except for BA, the only *C. nodosa* meadow.

This means that the positive feedback of sediment trapping is most likely not as strong as in the eastern meadows, further making these meadows less resilience. There is a plethora of other feedback mechanisms, which effects and differences on seagrasses along the coast are more difficult to evaluate.

Overall, these results confirm that besides the spatial variability of seagrass temporal trends at decadal temporal scales described in the literature, there is also spatial variability of seagrass dynamics at centennial and millennial scales. The main spatial differences are inter-regional, between the meadows along the mainland coast and the island although there are also differences between local sites that seem mostly dependent on the natural ecological/environmental background of each site. This highlights the critical need for local-regional assessment for management. So, does this mean that drivers of change are essentially local as some researchers have previously stated? Large-scale climate drivers do not influence any seagrass meadows? This will be discussed in section 3.

## 2.3. Changes in the community structure

Paleoecological studies in seagrass meadows should further focus on understanding how past environmental changes affected the whole community inhabiting the meadows and their interactions. Community compositional change over time can provide early warning diagnostic signals of approaching critical transitions, after which sequential changes may be triggered in other ecosystem attributes (Doncaster et al., 2016; Berdugo et al., 2020). Changes in the community composition and diversity have been observed to influence ecosystem functioning as much as other disturbances (Tilman et al., 2012). Community composition also affects the community resilience against disturbances, for example, epiphytic grazers have a fundamental role in seagrass beds, their consumption of seagrass epiphytes lead to an increase in light availability, which reduces the vulnerability of seagrass to other stressors (O'Brien et al., 2018b and other references therein). The abundance of these mesograzers is regulated by several complex interacting feedbacks between the seagrass plant, water-column nutrient concentrations, and the top-down control of predator abundance (Maxwell et al., 2016).

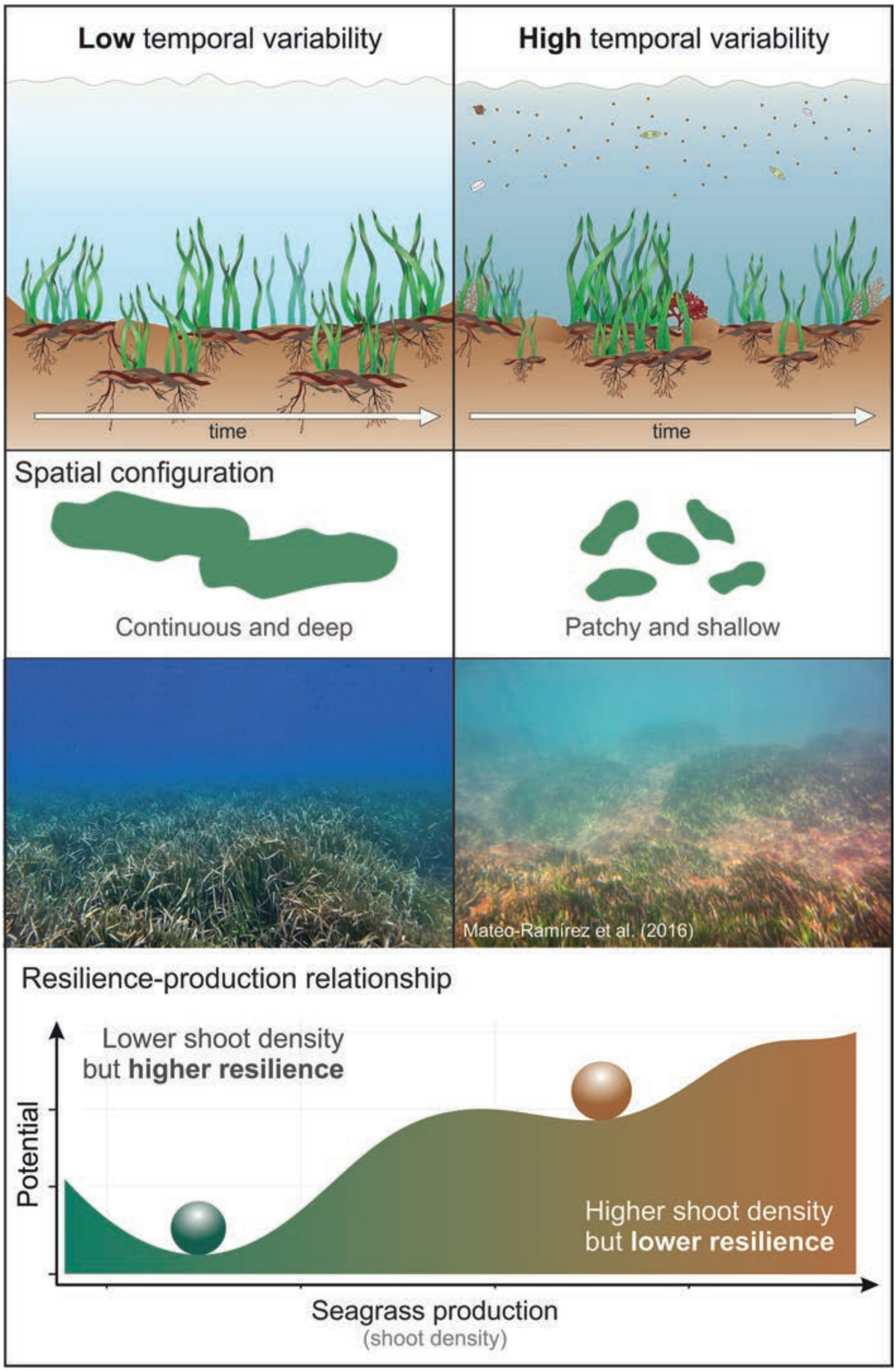
Within the frame of this thesis, long-term dynamics of the phototrophic community composition were studied using sedimentary pigments as proxy in Cabrera Island (**chapter 2**). The main compositional change observed was a recent increase of the dinoflagellate biomass over the last 150 years (as indicated by the pigment diadinoxanthin and dinoflagellate cyst concentrations). Moreover, the dinoflagellates increase seemed ultimately mediated through an increase of the energy influx, due to higher solar irradiance and atmosphere temperature, increase in temperature most likely due to the anthropogenic global warming. In the previous section, the long-term temporal data of seagrass production in the pristine island of Cabrera showed no clear common temporal trend between cores. Despite this, the compositional change in the community towards a higher abundance of dinoflagellates observed in all cores from Cabrera Island could be an early warning of a critical transition driven by an increased energetic influx, due to an elevated solar irradiance and seawater warming. Dinoflagellates can produce and accumulate high amounts of UV-absorbing photo-protective compounds (Hanna & Sigleo, 1998), which could help them thrive under periods of increased solar irradiance. Ocean temperature has risen as the atmosphere warmed (Levitus et al., 2000), a rise especially acute in the Mediterranean Sea partly due to its semi-enclosed nature (Templado, 2013). Surface warming increases the vertical density stratification, which reduces mixing between the surface and deeper water layers and, as a consequence, the nutrient supply from deeper layers to phytoplankton living in surface waters is reduced. Smaller, non-siliceous, and motile phytoplankton groups such as flagellates and dinoflagellates are expected to be favoured under this situation; a change that has been observed over the last decades in the NW Mediterranean in relation to climate forcing (Goffart et al., 2002; Marty et al., 2002). The warming Mediterranean also allows the successful establishment of tropical species which may arrive accidentally with ship ballast (Templado, 2013). The critical transition towards warmer and tropicalized seagrass ecosystem in the Cabrera Island, that was probably early indicated by the increase of dinoflagellates, is likely currently occurring as attested by the presence of *Halimeda incrassate*, invasive and tropical algae, first observed in Es Port Bay in 2016 (Zabarte Maeztu, 2017). Given the potential of this algae to deeply alter the ecosystem services and functioning (Alós et al., 2018), its spreading in meadows of Cabrera Island is likely a sign confirming that these seagrass meadows are currently undergoing a phase shift. Changes in the community composition have also been reported for *P. oceanica* meadows located in Liguria (Italian coast) where long data series reveal a recovery of the seagrass areal extent since 2009 but, at the same time, the meadow is being slowly substituted by *Caulerpa cylindracea*, which most likely indicates the transition towards a different basin of attraction (Bianchi et al., 2019). The decline and replacement of seagrass species have been observed to affect the associated faunal assemblages, which affects ecosystem functions such as the secondary productivity (Micheli et al., 2008).

Global warming might disrupt seagrass species interactions and community composition at local scales (e.g. Micheli et al., 2008), which can also have consequences for the stability of the ecosystem, specifically, communities' resilience is expected to decrease (Emmerson et al., 2005). Therefore, even if the long-term seagrass production may show an increase over time, which initially would not be a red flag, as this enhanced production is accompanied by compositional changes of the community at all sites of the island, the seagrass meadows in Cabrera Island may be undergoing a gradual change getting closer to a critical transition.

These results emphasize the importance of a multidimensional assessment of the ecosystem to get an adequate view of their complex responses, as the environmental change is also multidimensional (Donohue et al., 2016). In other words, changes of an ecosystem should be studied at several levels, from individual key engineering species to the whole community, therefore studying several diagnostics, such as the stability of ecosystem functions and the community composition. By doing that, we could better detect critical transitions and signals of resilience.

## 2.4. Conceptual model of seagrass long-term dynamics

By integrating the acquired knowledge in this thesis about the long-term seagrass dynamics, we could classify the meadows of study into two broad categories (Fig. 7). On one side, there are seagrass populations overall forming denser, but also patchier and shallower meadows. These meadows show a higher temporal variability of their production and also, lower resilience, being located in turbid and nutrient-rich waters, which receive higher loadings of terrestrial material, more specifically the western side of the Andalusian coast and in the Es Port Bay of Cabrera. On the other side, some populations form less dense, more continuous meadows reaching deeper areas. The temporal variability of seagrass production is lower, and the ecosystem resilience is higher in this second category, which encompasses meadows located in clearer and nutrient-poor environments, specifically in the eastern side of the Andalusian coast and in the Santa Maria Bay of Cabrera. Moreover, in Santa Maria Bay, there seems to be a depth gradient regarding the long-term dynamics, where the seagrass seems more productive, but also less stable, at shallower depths. A similar classification regarding seagrass resilience and the prevailing environmental conditions (although evaluated for shorter time scales) was observed and proposed by Jenkins et al. (2015) for the seagrass *Heterozostera nigricaulis* in Australia. They also observed that the more resilient meadows were located in areas with overall lower fluvial inputs. Accounting for the specific long-term seagrass dynamics provides an essential understanding of seagrass meadows, complex systems which management requires as detailed background knowledge.



Mateo-Ramírez et al. (2016)

**Figure 7.** Long-term dynamics of seagrass meadows vary among locations for *Posidonia oceanica* in the western Mediterranean. Populations in clearer, nutrient-poorer environments, which form continuous and deeper meadows, are less temporally variable, have lower shoot density, but their resilience is higher. On the other hand, populations living in turbid, nutrient-richer environments, which meadows are patchier and shallower, are also more temporally variable; and although having average higher shoot density, their ecosystem resilience to stressors is lower.

## 3. LONG-TERM CAUSES OF CHANGE AND THEIR RELATIVE INFLUENCE

Multiple, interacting drivers cause the majority of changes in ecosystems. Understanding the changes that ecosystems have undergone requires identifying the drivers behind these changes as well as untangling their effects. This is important to develop specific efficient management strategies and, also, assessing the long-term influence of climate on seagrass change is critical to estimate the effects of future climate change scenarios. So far, predictions of seagrass decline under different climate change scenarios are mainly based on seagrass losses associated with extreme weather events (Díaz-Almela et al., 2009; Marbà & Duarte, 2010; Rasheed & Unsworth, 2011; Jordà et al., 2012) and on mesocosms experiments on thermal limits (Olsen et al., 2012). The influence of long-term climate on seagrass change over centuries and millennia that is presented here is unprecedented, and it may help to refine predictions of seagrass change under global climate change and local impacts.

Some studies point to both global climate and local factors as the drivers behind the regression trend currently observed for seagrasses (Orth et al., 2006a; Boudouresque et al., 2009; Waycott et al., 2009; Bianchi et al., 2011; Marbà et al., 2014; Burgos et al., 2017). However, other studies that observe currently stationary or increasing local trends in seagrass meadows question the magnitude of this decline and deny the plausible role of large-scale climate factors in seagrass regression. Hence, they consider that causes behind the declining meadows are only or mostly local and could be simply managed at a local-level (González-Correa et al., 2007; Bonacorsi et al., 2013; Guillén et al., 2013; Telesca et al., 2015). In **chapter 4**, we tried to shed light on this debate by using paleoecological data and GAM models to assess the relative importance of local versus large-scale drivers in long-term seagrass production and between different areas.

Local processes driving seagrass change are direct sources of disturbance, which are more likely to be human-derived during recent periods. The main local factor with a ubiquitous, although moderate, influence was terrestrial inputs. Its impact on the seagrass production was negative in meadows dwelling in lower-light and turbid waters (CA, ME, BA and SM05). Sites where production could be more easily affected by any further reduction in light as seagrasses are pushed towards their photosynthetic compensation point. However, on the rest of the meadows, where underwater light availability is naturally higher, the arrival of terrestrial material had a positive impact on seagrass production, which could be due to a beneficial effect from moderate inputs of nutrients together with the fluvial discharges,

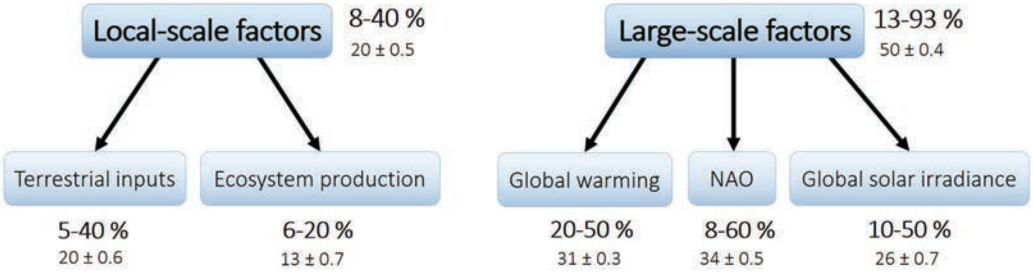


**Figure 8.** Diagram showing the range, mean, and coefficient of variation of the explained variance of seagrass paleoproduction by local and large-scale factors as calculated using GAM models in chapter 4.

nutrients that can enhance seagrass production (McGlathery et al., 2007). The global rise of temperature due to anthropogenic emissions of greenhouse gases had a negative effect on those meadows growing in turbid conditions that were also negatively affected by natural high fluvial loadings. Seagrass photosynthesis could not achieve the increased carbon demand derived from the temperature rise due to turbid waters and reduced light availability, likely leading to negative carbon balance. However, in meadows where underwater light was not naturally limited, global warming had a positive effect, at least until very recently. These results suggest that seagrass meadows in which light availability was naturally compromised are more sensitive to further disturbances, hence, less resilient to river run-off and rises in seawater temperature, pointing to a synergistic interaction between the local, historical environmental conditions and large-scale climate changes. The lower resilience of meadows growing under turbid conditions to additional stress has also been observed at shorter temporal scales in previous research (Yaakub et al., 2013; Fraser et al., 2014).

Large-scale processes are affecting seagrass change indirectly, and they can be both natural and anthropogenic. In **chapter 4**, the large-scale factor that could be considered anthropogenic is the global rise of atmosphere temperature linked with the greenhouse gases rise. Overall, the results of GAM models in **chapter 4** revealed that global climate factors did explain a significant, although variable (13 to 93%), part of the variability of the seagrass production for most of the meadows (Fig. 8). In **chapter 1**, the explained variance of seagrass production by local and large-scale factors was also assessed through partial RDA in combination with Monte Carlo permutations, revealing similar explained variances between local, large-scale factors and their interactions. Previous studies trying to assess the importance of climate variability on seagrass change over shorter periods (decadal scales) also found contrasting results. Some studies reported strong correlations between seagrass cover and environmental variables, such as tidal exposure, global solar radiation, local air temperature, rainfall, fluvial discharges, etc (Marbà & Duarte, 1997; Peirano et al., 2011; Rasheed & Unsworth, 2011; Unsworth et al., 2012; Marques et al., 2014), while others found that climatic variables explained only a small proportion of the observed seagrass variability (Terrados & Medina-Pons, 2011; Alonso Aller et al., 2019). In both, **chapter 1 and 4**, results pointed to a varying influence of the considered factors over time, standing out the cyclical contribution of the terrestrial material to seagrass production, most likely related to regional climate changes, and the increasing influence of the global temperature rise over the last century. These results are in line with what was recently observed by Halpern et al. (2019), who reported climate stressors to be the dominant drivers of change in coastal ecosystems, which included seagrass meadows.

The interaction of climate change and local disturbances over the last century may be driving seagrasses meadows to a threshold which critical value could be different and specific to local contingencies, such as the environmental conditions and legacies of past disturbances. Long-term legacies have also been proven to shape and affect current processes and attributes of current terrestrial and marine ecosystems (Parravicini et al., 2013; Monger et al., 2015; Svenning et al., 2015; Nowicki et al., 2019). In the Cabrera Island, where seawater temperature does not show a clear long-term increase over the last 150 years (Cisneros et al., 2015) and human disturbance has been comparatively and significantly lower than along the mainland coast of Andalusia, long-term legacies may have not acutely affected the ecosystem. Therefore, seagrass meadows will likely take longer to cross a tipping point. Along the highly anthropized Andalusian coast, according to the overall results of this thesis, abrupt changes will likely be faster and happen sooner in those seagrass meadows chronically exposed to low light levels, i.e. receiving naturally higher fluvial discharges, hence living in more turbid waters.

The GAM models of AG and DE meadows showed high levels of unexplained variability (63 and 85%, respectively). Considering that these two meadows had the longest temporal series, part of this unexplained variability could be attributed to an underestimation of the influence of some of the considered factors due to a problem of pairing time series in older samples because of higher age uncertainties. The remaining unexplained variability (between ~10-40% in cores covering shorter time periods) could be further explained by other climatic or local environmental factors influencing seagrass change, such as sea level rise, herbivory, hydrodynamism, local human disturbances, etc. These factors were not included in these models.

Despite the lack of widespread spatial declining trends, the results of this thesis indicate that even though seagrass regression seems spatially variable, it cannot be only ascribed to local causes and provide evidence to consider large-scale factors as feasible causes explaining part of past and current declining trends. In **chapter 3**, seagrass production in Andalusia was negatively correlated with the northern hemisphere temperature while in Cabrera, it was positively correlated, pointing to temperature as a key driver. However, local and global causes of seagrass long-term dynamics seem to have spatially different relative weights. The influence of climate seemed especially crucial in meadows surrounded by more turbid waters and under the influence of higher fluvial discharges.

# GENERAL CONCLUSIONS

- New proxies have been revealed as useful for the understanding of the recorded sedimentary processes in seagrass deposits: (1) several proxies proved to be indicators of the seagrass paleoproduction, which included the stable carbon stable isotope composition of the seagrass sheaths, as well as the combination of several organic compounds (aromatics, phenols, carbohydrates and lipids) identified by infrared spectroscopy; (2) sedimentary pigments were useful proxies of changes in the abundance and composition of all the primary producer's inhabiting seagrass meadows; (3) the proportions of debris from different seagrass organs (sheaths, rhizomes and roots) were related with an aboveground/belowground organ ratio, mainly influenced by the nutrient availability.

- The Fourier-Transformed Infrared spectroscopy (FTIR) technique proved to be a very valuable tool to identify the different components of seagrass deposits, especially those of biological origin, allowing a general overview of the main organic compounds preserved in the deposits, such as aromatics, phenolics, polysaccharides, linings, lipids and nitrogen-containing compounds.

- All the environmental processes identified in seagrass deposits were somehow related with the primary producers' production: the balance between algae and seagrass production, i.e. the different sources of organic matter (related as well with the influence of terrestrial inputs), the whole ecosystem production and the production of the seagrass plant itself.

- The same ecological functions, such as seagrass production, were recorded in the seagrass deposits of different regions through different proxies. In other words, the same proxy was not always indicative of the same process or function. This result underlines the complexity of these ecosystems, with different environmental factors and processes influencing the meadows, and translates into the need of using a multiproxy approach for a reliable paleoecological interpretation.

- Long-term oscillating dynamics seem to be the natural characteristic of the seagrass meadows in response to environmental variability, although this dynamism varied spatially, with the main spatial differences being inter-regional. There are also differences between local sites that seem mostly dependent on the natural ecological/environmental background of each site, differences that revealed a trade-off between long-term stability and production: the more productive a meadow is, the more oscillating are its long-term dynamics.

- The main common long-term trend revealed by the paleoecological reconstructions of this thesis is a recent decrease in seagrass production since ~1850 AD along the mainland coast. However, the results reveal increasing or stable trends in meadows of Cabrera Island for the same period. In Cabrera, the long-term change observed was a recent increase of the dinoflagellate biomass towards present over the last 150 years.

- The major factors responsible for long-term variability of seagrass ecosystem dynamics were multiple and of both, local and large spatial scale, highlighting the influence of terrestrial material and the energy influx, which encompass the recent global warming, regional atmospheric patterns and natural climate changes modulated by global solar irradiation. However, the balance between the contribution of local and large-scale drivers varied spatially.

- Fluvial discharges had a ubiquitous, although moderate, influence on long-term seagrass production. The global rise of temperature due to anthropogenic activities had different impacts on seagrass production. Seagrass meadows where light availability was compromised were more sensitive to rises in seawater temperature. Other climate factors, such as the North Atlantic Oscillation mode, also had a significant influence, with overall higher seagrass production during negative NAO phases, humid periods likely increasing nutrient availability from upwelling waters and terrestrial discharges.

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# SUPPLEMENTARY MATERIAL

# APPENDIX A

**Table S1.** Results of Monte Carlo permutation tests (n=999) on pRDA models. Five pRDA models were run, one per PC, so one of the PC was the response variable in each of them. All models had the same four explanatory variables: TSI, NH temperature, PC1m and PC2m. All pRDA models had sample ages partialled out as a covariable. Monte Carlo permutation tests were used to test the significance of the model and of each predictor variable (999 permutations), obtaining the partial explained variation and the significance for every explanatory variable. Levels of significance: *P≤0.05, **P≤0.01, ***P≤0.001.

| Response variables | % variance explained | Model p-value | Significant terms | % variance explained by each term | Terms p-value |
|---|---|---|---|---|---|
| PC1 (OM accumulation) | 15.3 | 0.001 | TSI | 2.87 | 0.001*** |
| | | | PC1m | 8.72 | 0.001*** |
| | | | TSI*NH | 1.94 | 0.007** |
| PC2 (sheath/ belowground organs) | 10.5 | NS | | | |
| PC3 (soil erosion) | 36 | 0.001 | TSI | 7.6 | 0.001*** |
| | | | PC1m | 13.57 | 0.001*** |
| | | | PC1m*PC2m | 4.03 | 0.002** |
| | | | TSI*NH | 1.71 | 0.017* |
| | | | TSI*PC1m | 1.36 | 0.042* |
| | | | NH*PC1m | 2.05 | 0.011* |
| | | | TSI*NH*PC1m | 1.86 | 0.017* |
| PC4 (productivity) | 21.1 | 0.001 | TSI | 3.16 | 0.014* |
| | | | PC1m | 5.04 | 0.001*** |
| | | | TSI*NH | 3.33 | 0.008** |
| | | | TSI*PC1m | 3.58 | 0.001*** |
| | | | NH*PC1m | 2.03 | 0.043* |
| | | | PC1m*PC2m | 1.82 | 0.043* |
| PC5 (phosporus availability) | 23.7 | 0.001 | NH | 1.93 | 0.043* |
| | | | PC2m | 4.14 | 0.004** |
| | | | PC1m | 4.9 | 0.005** |
| | | | NH*PC2m | 7.11 | 0.001*** |
| | | | PC1m*PC2m | 2.38 | 0.029* |

TSI stands for Total Solar Irradiation, given as the difference respect to the value of the Physikalisch-Meteorologisches Observatorium Davos (PMOD) composite during the solar cycle minimum of the year 1986 AD (1365.57 W/m$^2$; Steinhilber *et al.*, 2012)

NH is the Northern Hemisphere temperature anomalies in ºC. It is ice-core-derived and from the base year of 1961–1990 (Kobashi *et al.*, 2013).

PC1m and PC2m are principal components from heavy metal abundances in sheaths also analysed in Core 2000 (Serrano *et al.*, 2011). PC1m, considered to be related to anthropogenic activities in the catchment, and PC2m, related to metals with a lithogenic origin.

# APPENDIX B

## Coring procedures

Coring was conducted in June 2015. Cores were collected by scuba divers using high density PVC pipes (1 to 1.5 m length, 7 cm internal diameter) fitted with core catchers and a serrated leading edge. Pipes were slowly hammered into the *P. oceanica* mats with gentle rotation to minimize core compression. The compression of the cores was measured by measuring the collected sediment length and the height of the pipe that remained outside the sediment. The observed degree of core shortening was within the expected range (up to 30%; Morton & White, 1997), averaged 20.5 % (SD= 13.4%) and ranged from 5.6% to 42%. Despite of the precautions taken, the compression in the SM05 core was exceptionally high, at 42%. An exponential decompression function was applied to correct for core shortening (Morton & White, 1997; Serrano, Mateo, Renom, & Julià, 2012).

## Sedimentology, geochemical analyses and core chronology

Once obtained, cores were taken to the laboratory and stored at 4ºC until analysis. Within 5-10 days after sampling, the cores were cut longitudinally and opened into two halves. One-half of each core was photographed at high resolution and analysed at 1cm-intervals by X-ray fluorescence (XRF) non-destructively using an AVAATECH core scanner (10–30 kV; 10–30 s measuring time), for determination of the elemental composition (CORELAB laboratory, University of Barcelona). The other half-core was cut into 1 cm-thick slices and divided into subsamples for subsequent analyses. Subsamples were taken from every interval along the first 30 cm and from every other interval below 30 cm. Subsamples from one half-core were dried at 60ºC until constant weight to determine the dry bulk density, and then alternate intervals were homogenized using an automated agate mortar (Mortar Grinder RM-200 RETSCH).

Organic matter content (OM) was estimated by mass-loss-on-ignition at 550ºC for 4h (Heiri et al., 2001). Sample grain size was determined using a laser-diffraction particle analyser (Mastersizer 2000, Malvern instruments Ltd., UK) after digestion with 30% hydrogen peroxide (Kunze & Dixon, 1986). Samples were then sieved (1-mm mesh) to remove the coarse fraction prior to grain size analysis.

Carbon and N elemental and isotopic composition of sediment samples was determined at UH Hilo Analytical Laboratory, University of Hawaii at Hilo, on a Thermo-Finnegan Delta V IRMS isotope ratio mass spectrometer coupled with a Costech elemental analyser. Each sample was analysed twice; before acidification for N content and stable $\delta^{15}N$ isotopes, and post-acidification with 4M HCl for organic C content and stable $\delta^{13}C$ isotopes. Carbon and nitrogen isotope ratios were expressed in standard δ notation (‰) relative to the Vienna PeeDee Belemnite and atmospheric $N_2$ standards, respectively. The analytical precision using standards was estimated as ± 0.14‰ for $\delta^{13}C$ and ± 0.08‰ for $\delta^{15}N$. Relative elemental proportions (% dry mass) of C and N also showed good reproducibility (± 0.4 and ± 0.01%, respectively).

For GDGT analysis, freeze-dried subsamples were extracted with an Accelerated Solvent Extractor (DIONEX ASE 200) using a mixture of dichloromethane (DCM) and methanol (MeOH) (9:1 v/v) at 100 ºC and 7.6 $\cdot x10^6$ Pa. GDGTs in centrifuged samples were quantified using an internal standard (C46 GDGT) according to Huguet et al. (2006). The extracts were separated into non-polar, alkenone and polar fractions over an column with activated alumina, eluting with hexane:DCM (9:1 v/v), hexane:DCM (1:1 v/v) and DCM:MeOH (1:1 v/v), respectively. Four to nine samples of *P. oceanica* sheath debris were taken per core and dated using $^{14}C$ accelerator mass spectrometry (DirectAMS laboratory) following standard procedures (Karlén et al., 1968; Stuiver & Pollack, 1977). Samples were pretreated as indicated in Belshe et al. (2019). The uppermost 30 cm of each core was dated by quantification of $^{210}Pb$ activities using alpha spectrometry using a PIPS detector (CANBERRA, Mod. PD-450.18 AM) at the Autonomous University of Barcelona's Environmental Radioactivity Laboratory (Appleby & Oldfield, 1978). Details of $^{210}Pb$ dating method can be consulted in Belshe et al. (2019).

Age-depth models were developed using a Bayesian modelling approach (*Bacon* package within R statistical environment, Blaauw & Christen, 2011). Radiocarbon dates were expressed as calibrated years before present (cal. yr BP). Dates were calibrated using the *marine 13* calibration curve (Reimer et al., 2013) and a correction for the local marine reservoir effect (mean ± SD; ΔR = 26 ± 24 years, Riera Rullan, 2016).

## Fossil pigment analysis

Frozen sediment samples were freeze-dried (24 h, 0.1 Pa) and pigments extracted from ~1–4 g sample dry mass using a standard mixture of acetone : methanol : water (80 : 15 : 5, by volume) (Leavitt and Hodgson, 2001). Filters were washed with three 1-ml volumes of fresh extraction solution and extracts solutions combined to achieve ~95% complete extraction and minimal derivative formation in comparison with more exhaustive protocols. Combined extracts were filtered through a 0.2 $\mu$m pore chemically-resistant membrane filter, evaporated to dryness under a stream of inert $N_2$ gas, and stored under $N_2$ at -20ºC. All extracts were conducted under low indirect lighting using $N_2$-degassed solvents.

Prior to analysis, dried extracts were dissolved into a known volume of injection solvent containing an internal reference standard (3.2 mg/l) of Sudan II (SigmaChemical Corp., St. Louis, Mo.). Pigments were separated using an Agilent model 1100 HPLC with an in-line photodiode array detector and fluorescence detector. Pigments were tentatively identified on the basis of chromatographic position and spectral characteristics in comparison with authentic standards (DHI Netherlands) and a library of pigment isolates from pure algae cultures. Pigment concentration was expressed as nmoles pigment $g^{-1}$ organic matter, a metric known to be linearly related to the abundance of primary producers in whole-ecosystem experiments and mass budget studies (Leavitt & Hodgson, 2001).

Lutein from chlorophytes and higher plants, as well as zeaxanthin from cyanobacteria were incompletely resolved on our HPLC system and are presented together as lutein-zeaxanthin (Leavitt & Hodgson, 2001).

## Organic-walled dinoflagellate cysts analysis

The average sample volume used for the analysis was 3.52 $cm^3$. The palynological extraction was performed following standard procedures (i.e., HCl, NaOH and HF attacks to eliminate carbonates, humic acids and silicates, respectively). Density separation using sodium polytungstate (SPT, specific gravity of 2.4) was performed to concentrate the palynomorph content. Finally, residues were sieved through disposable nylon meshes (125 and 10 µm) and the 10–125 µm fraction was retrieved. The final residues were mounted on slides using glycerol. Known concentration of *Lycopodium clavatum* spores were added to each sample prior to processing to allow calculation of fossil concentrations as number of dinocysts per $cm^3$ of sample. Dinocysts were identified and counted using light microscopy at ×400 magnifications.

## Numerical procedures

The fact that fossil pigment data are reported in units of concentration (i.e., relative contributions on a whole), and composed of positive values, are key indicators of compositional data (Aitchison, 1986). The relevant information for each variable in a compositional dataset is in the ratios between all variables, and the best available transformation for compositional data is the isometric log-ratio (ilr) (Egozcue et al., 2003; Filzmoser et al., 2010). If compositional data (expressed in concentrations or log-transformed) are used in classical analyses based on Euclidean space, i.e., in “classical” biplots, distorted structures often appear. In this study, almost all the variables were arranged only in a half-plane which did not reflect the real underlying relationships (Fig. S3A and B, Filzmoser et al., 2010; Filzmoser, Hron, & Templ, 2018). For this reason, ilr-transformed pigment data was used, and resulted in an open ordination display rather than variables arranged in a half-plane (Fig. S3C).

Zeros were replaced because of the use of log-ratio transformations using a robust imputation method –*imputeBDLS*– from robcompositions package (Templ et al., 2011). This decision was based on the assumption that null values were rounded zeros, i.e., concentrations below the detection limit rather than true absences. Subsequently, associations in pigment concentration data were studied using a robust PCA ($\text{PCA}_{\text{pigments}}$) via *pcaCoDa* command in "robcompositions" package (Templ et al., 2011). Use of a robust method (i.e., a robust covariance matrix of the ilr-transformed data) reduces the influence of data outliers (Filzmoser et al., 2009). This PCA performs an isometric log-ratio (ilr) transformation of the dataset and then converts the data back to a centred log-ratio (clr) for interpretation. Interpretation of covariance clr-biplots is slightly different from that of general biplots as pointed out by Daunis-i-Estadella et al. (2011). The principal elements of interpretation are the length of the rays and the links between rays: the length of the rays is proportional to the variability of the clr-variable; if rays are aligned, the relationships between the parts are linear, whereas orthogonal links (connecting lines between ends of rays) indicate that the participating pairs of rays are uncorrelated, so the factors or processes associated with the participating pairs are probably independent. Also, samples orienting in the direction of single arrows correspond to observations with high abundance of the respective variables (Filzmoser et al., 2018).

To determine which environmental variables were the most influential on pigment marker composition, another robust PCA was run including both local factors and global climate indicators ($\text{PCA}_{\text{environmental}}$). Local factors included biotic-related ones such as total primary production (as chl-*a*, β-carotene and OM), nutrient cycling and organic matter supply (C and N stable isotope values and BIT index), as well as abiotic descriptors (sample grain size and elemental composition, including C, N and XRF-measured elements). Global climate external factors included Total Solar Irradiance (TSI, Vieira et al., 2011), Northern Hemisphere Temperature (NHT, Kobashi et al., 2013) and the North Atlantic Oscillation (NAO; Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012) - NAO is an atmospheric mode affecting the hydrological variability in the western Mediterranean (Roberts et al., 2012). Grain size distribution and elemental compositions were included considering the compositional character of each group. This analysis was conducted using the *pcaCoDa* function in the robcompositions package, as it allows more than one group of compositional parts to be considered through the use of "mult_comp" argument. The rest of the variables were scaled by subtracting the median and dividing by the median absolute deviation using the *robustscale* function in the quantable package (Wolski, 2018). Dinocyst concentrations could not be included in this PCA because data are only available for EP05 and SM25 cores and, moreover, for a reduced number of samples. The number of principal components retained was determined by the overall shape of the scree plots, retaining all components within the sharp descent.

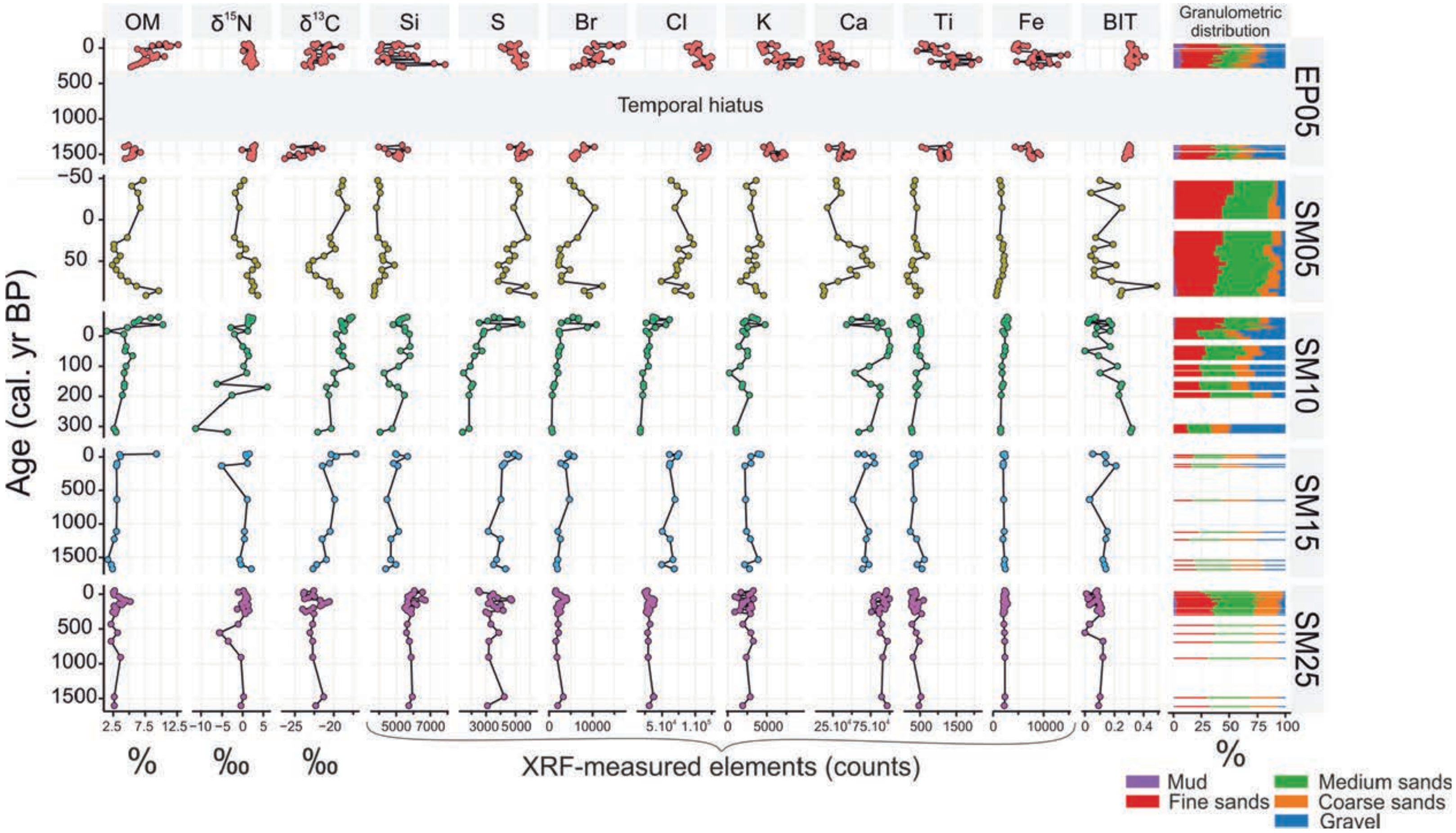


**Figure S1.** Descriptive variables along the cores plotted against age: sediment organic matter content (OM), carbon and nitrogen stable isotopes, XRF-measured elements (Fe, Si, Ti, K, Ca, S, Cl and Br), BIT index and grain size distribution.

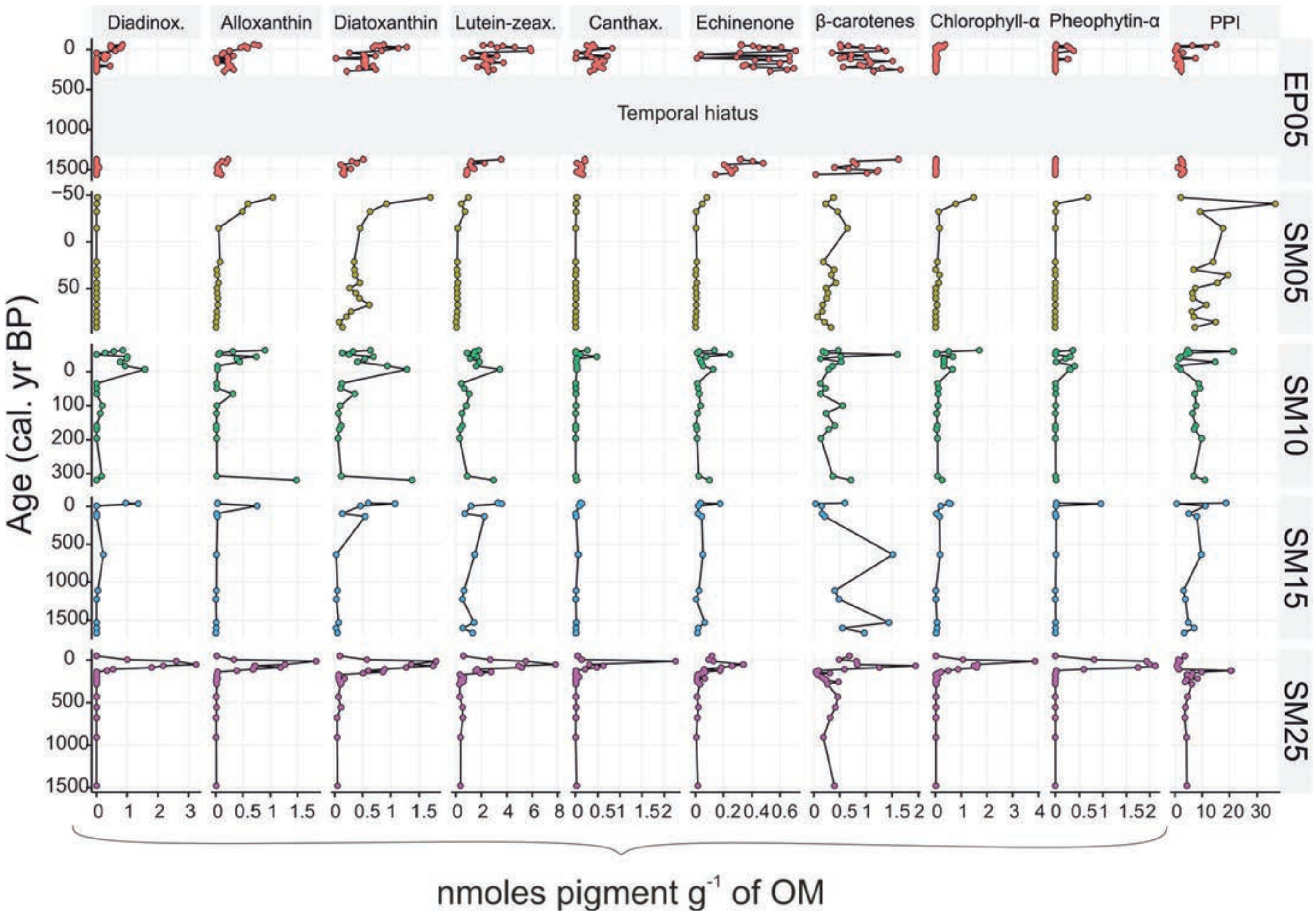


**Figure S2.** Profiles of pigment concentrations plotted against age for each core. PPI stands for pigment preservation index and it was calculated as the ratio between chl-*a* and pheophytin *a*.

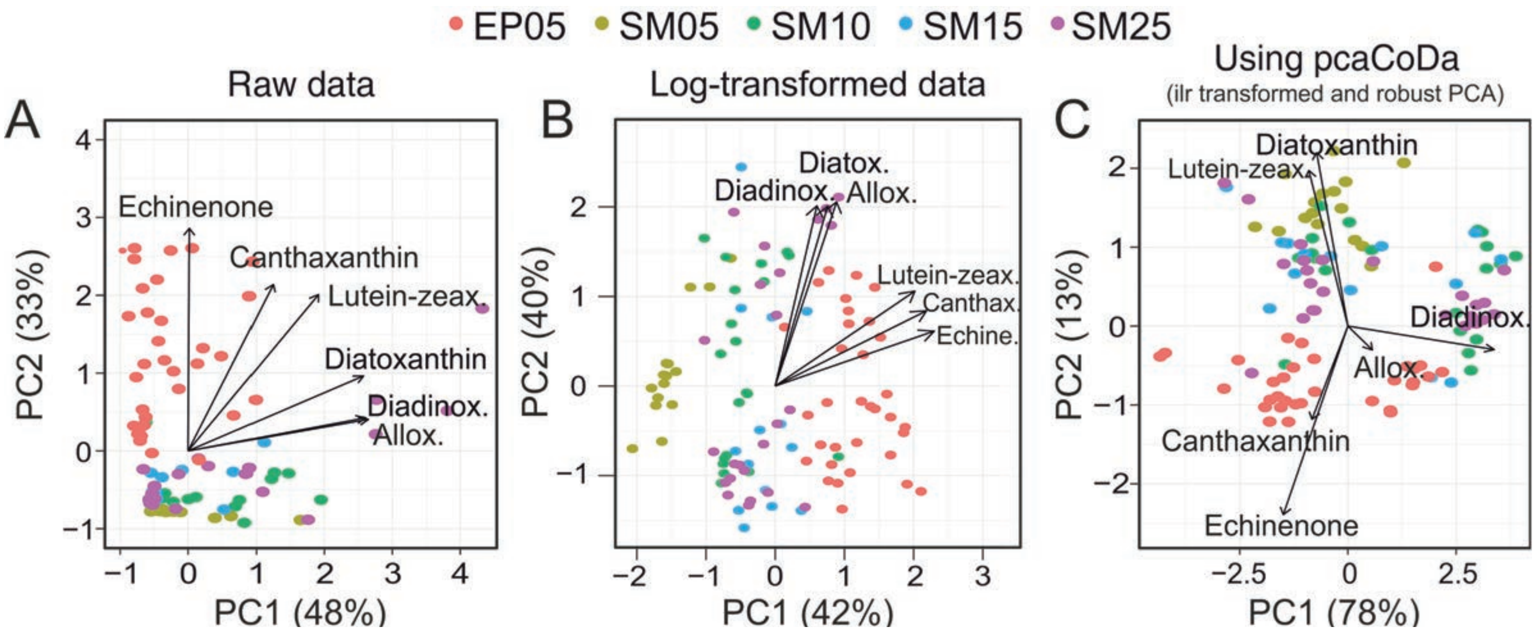


**Figure S3.** Biplots for the Cabrera pigment data set based on the raw data (A), log-transformed variables (B) and on the ilr-transformed data back transformed to clr (C).

# APPENDIX C

## Materials and methods

Practices for minimising core compression were used (i.e. specially designed cutting edge, coring at a low descent rate using gentle rotation). The compression of the cores was measured by calculating the difference between the part of the core that remained outside the sediment and the height of the empty space that remained inside the tube. The overall degree of core shortening was within the expected range (up to 30%; Table 1; Morton & White, 1997), except for core SM05 (42%). An exponential decompression function was applied to correct for gradual shortening as coring resistance increases with depth (Morton & White, 1997; Serrano et al., 2012).

For the elemental and isotopic (C, N) composition, each sediment sample was analysed twice; before acidification (N isotopes) and after acidification with 4M HCl (organic C isotopes). Carbon and nitrogen isotope ratios are expressed in standard δ notation (‰) relative to the Vienna PeeDee Belemnite and atmospheric $N_2$ standards, respectively. The analytical precision using standards was estimated as ± 0.14‰ for $\delta^{13}C$ and ± 0.08‰ for $\delta^{15}N$. Relative elemental proportions (% dry mass) of C and N also showed good reproducibility (± 0.4 and ± 0.01%, respectively).

The biplot of the PCA encompassing the whole set of cores showed a plausible artefact known as the Horseshoe Effect (Fig. S2), i.e. the second axis is curved and relative to the first, not being, therefore, a true secondary gradient (Lewis and Menzies, 2015). To allow the use of PCA, we decided to analyze each area of study separately: a PCA for the meadows located around Cabrera Island and growing on carbonate sediments ($PCA_{CAB}$) and another one for the meadows located along Andalusia and growing on more siliciclastic sediments ($PCA_{AND}$). Principal component analysis (PCA) was applied using the correlation matrix with a varimax rotation.

Prior to PCAs, all non-compositional variables were robustly scaled by subtracting from the values of each variable the median and dividing by the median absolute deviation by using the command *robustscale* in the “quantable” package (Wolski, 2018). PCA analyses were performed with the *pcaCoDa* command in the “robcompositions” package (Templ et al., 2011). This command allowed accounting for the compositional character of the log-ratios of XRF-elements intensities (Weltje and Tjallingii, 2008). This PCA performs an isometric log-ratio (ilr) transformation of the compositional variables and convert them back to a centred log-ratio (clr) for interpreting results (Filzmoser et al., 2018). Compositional variables had zeros replaced using a robust imputation method –*imputeBDLS*- from “robcompositions’” package for R (Templ et al., 2011).

The number of principal components to retain was determined by the overall shape of the scree plots.

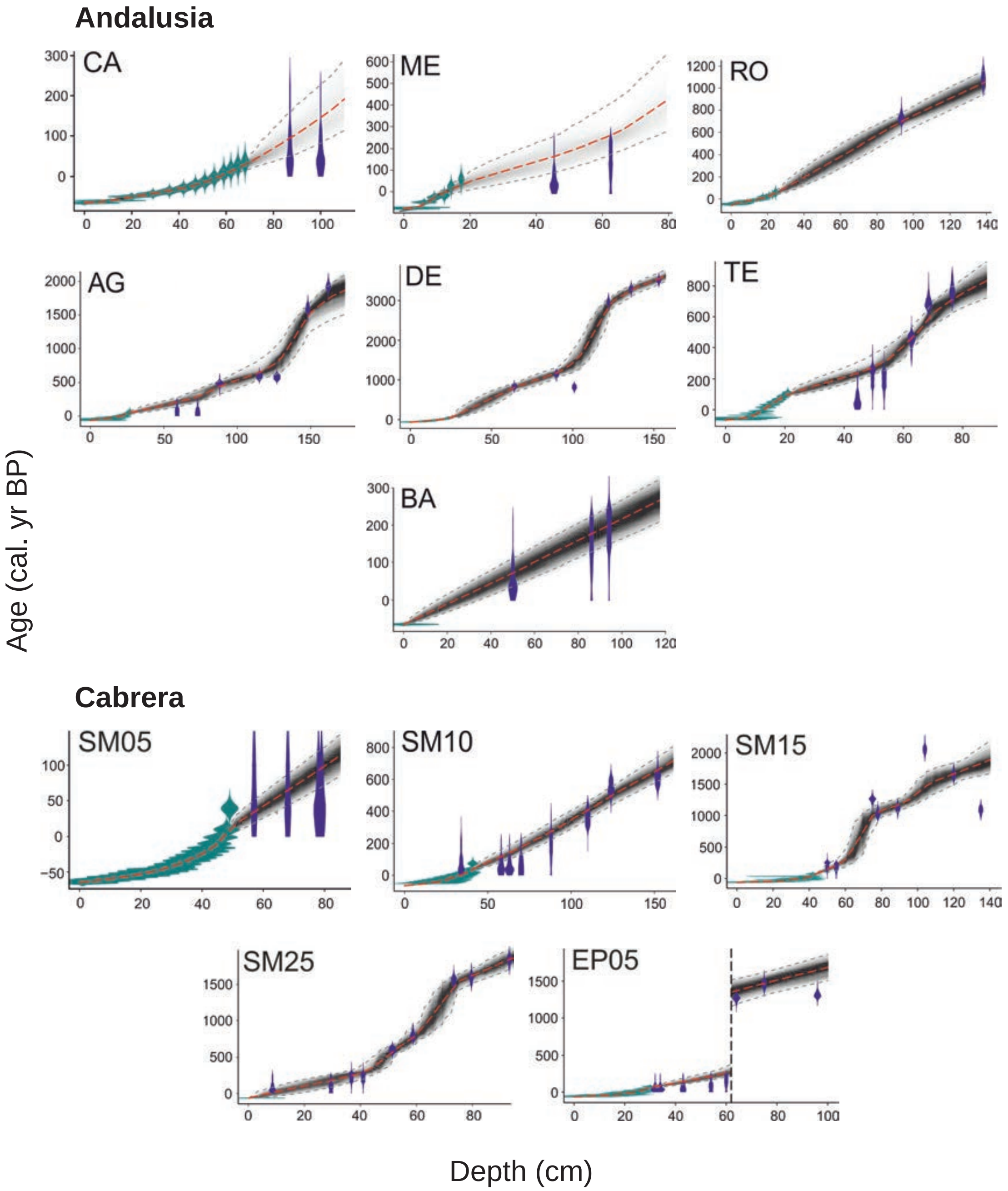


**Figure S4.** Bayesian age depth-models of seagrass cores using Bacon.R software (Blaauw & Christen, 2011). Lead-210 (in green) and radiocarbon (in blue) dates were included. Radiocarbon dates were calibrated using the *marine 13* calibration curve (Reimer et al., 2013) and corrected for a local marine reservoir effect for the Andalusian coast (ΔR = 2 ± 26 years, Siani et al., 2000) and Cabrera Island (ΔR = 24 ± 26 years, Riera Rullan, 2016). The red dashed curve shows the "best" model based on the weighted mean age for each depth. Individual radiocarbon dates are shown in probability density functions of calibrated ages. The grey area indicates the uncertainty envelope of the age model with grey dashed curves indicating the 95% confidence intervals.

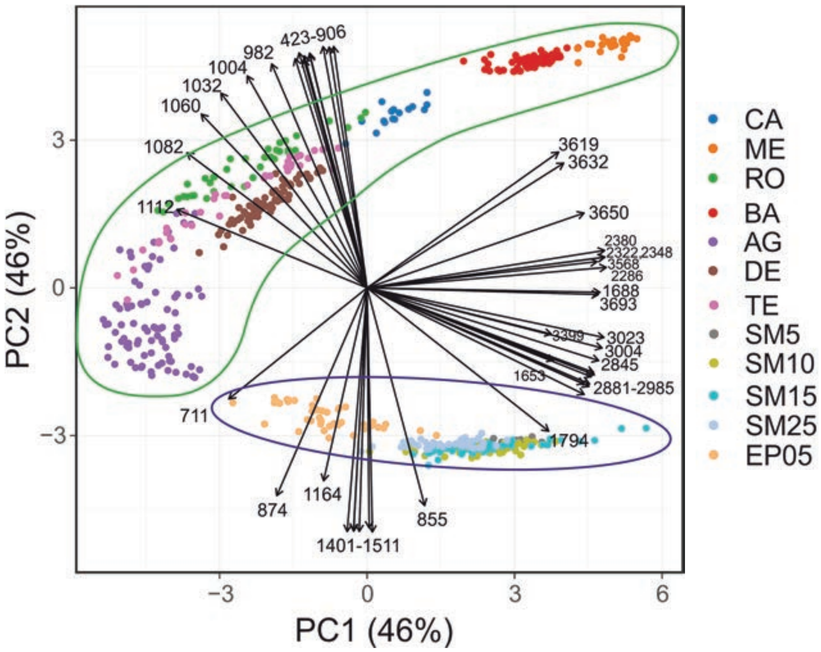


**Figure S5.** Biplot of the PCA encompassing the FTIR dataset for the whole set of cores. The blue ellipse corresponds to cores from the Cabrera Island and the green ellipse to those located along the coast of Andalusia.

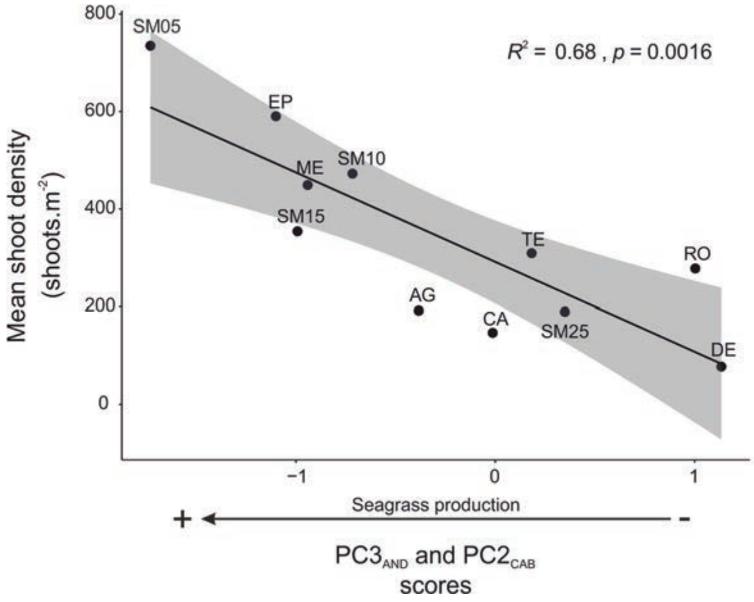


**Figure S6.** Linear correlation between current values (from 2000 to 2018) of PC3$_{AND}$ and PC2$_{CAB}$ scores (principal components related with seagrass production) and mean seagrass shoot density (mean values for temporal series between 2004 and 2018 for Andalusia – CAGPDS, 2018 – and between 2000 and 2007 for Cabrera – Marbà et al., 2002, 2005; Holmer et al., 2003; Terrados & Pons, 2008; Marbà & Duarte, 2010; Mazarrasa et al., 2017b –).

**Table S2**. Details of radiocarbon dates in the *P. oceanica* mat sediment cores retrieved in Cabrera Island and the Andalusian coast. The marine13.14C calibration curve was used for calibration and a local marine reservoir effect included (ΔR = 2 ± 26 years; Siani et al., 2000). The material dated was seagrass organic matter in all samples (*P. oceanica* in all cores except for BA, where material came from *C. nodosa*). AMS: Acceleration Mass Spectrometry; Cal.: dendrocalibrated.

| Core | Laboratory code | Depth (cm) | AMS $^{14}$C date (yr BP) | Cal. yr BP (2σ range) | Weighted mean age |
|---|---|---|---|---|---|
| **CA** | D-AMS 029722 | 87 | 186 ± 24 | 51 – 159 | 95 |
| | D-AMS 029723 | 100 | 351 ± 30 | 83 – 230 | 146 |
| **ME** | D-AMS 029653 | 44.6 | 339 ± 32 | 94 – 253 | 166 |
| | D-AMS 029654 | 61.4 | 515 ± 28 | 170 – 390 | 252 |
| **RO** | D-AMS 029737 | 92 | 1151 ± 28 | 561 – 741 | 665 |
| | D-AMS 029738 | 136 | 1501 ± 33 | 908 – 1114 | 1009 |
| **BA** | D-AMS 026924 | 50 | 334 ± 23 | 39 – 117 | 77 |
| | D-AMS 026922 | 86 | 524 ± 21 | 135 – 234 | 185 |
| | D-AMS 026923 | 94 | 567 ± 22 | 156 – 259 | 209 |
| **AG** | D-AMS 029647 | 59 | 471 ± 28 | 118 – 248 | 183 |
| | D-AMS 029635 | 73 | 454 ± 30 | 196 – 378 | 269 |
| | D-AMS 029648 | 88 | 868 ± 31 | 315 – 512 | 424 |
| | D-AMS 029636 | 115 | 1023 ± 28 | 532 – 819 | 639 |
| | D-AMS 029721 | 127 | 996 ± 25 | 619 – 1032 | 797 |
| | D-AMS 029637 | 148 | 2030 ± 31 | 1193 – 1636 | 1477 |
| | D-AMS 029649 | 162 | 2315 ± 29 | 1394 – 1930 | 1736 |
| **DE** | D-AMS 029641 | 64 | 1297 ± 29 | 679 – 906 | 798 |
| | D-AMS 029629 | 90 | 1578 ± 27 | 1036 – 1308 | 1168 |
| | D-AMS 029642 | 101 | 1273 ± 32 | 1209 – 1801 | 1465 |
| | D-AMS 029630 | 122 | 3178 ± 35 | 2564 – 3027 | 2822 |
| | D-AMS 029643 | 136 | 3435 ± 36 | 3091 – 3388 | 3253 |
| | D-AMS 029631 | 153 | 3614 ± 33 | 3414 – 3690 | 3548 |
| **TE** | D-AMS 029644 | 44.5 | 414 ± 30 | 235 – 373 | 300 |
| | D-AMS 029632 | 49.5 | 597 ± 27 | 270 – 417 | 343 |
| | D-AMS 029645 | 53.5 | 562 ± 29 | 307 – 459 | 384 |
| | D-AMS 029633 | 62.5 | 821 ± 28 | 435 – 588 | 499 |
| | D-AMS 029646 | 68.5 | 1135 ± 32 | 535 – 681 | 605 |
| | D-AMS 029634 | 76.5 | 1223 ± 27 | 650 – 813 | 728 |
| **EP05** | D-AMS 014002 | 32 | 398 ± 23 | 59 – 93 | 76 |
| | D-AMS 019447 | 34 | 379 ± 24 | 67 – 108 | 87 |
| | D-AMS 014003 | 43 | 467 ± 27 | 104 – 190 | 141 |
| | D-AMS 012768 | 54 | 502 ± 27 | 166 – 277 | 215 |
| | D-AMS 029626 | 60 | 545 ± 30 | 202 – 349 | 264 |
| | D-AMS 019448 | 64 | 1741 ± 28 | 1185 – 1531 | 1369 |
| | D-AMS 012769 | 75 | 1940 ± 26 | 1305 – 1620 | 1469 |
| | D-AMS 012770 | 96 | 1788 ± 29 | 1473 – 1473 | 1652 |
| **SM05** | D-AMS 012771 | 57 | 75 ± 26 | 19 – 51 | 34 |
| | D-AMS 012772 | 68 | 105 ± 28 | 43 – 87 | 65 |
| | D-AMS 013117 | 78 | 366 ± 25 | 67 – 120 | 93 |
| | D-AMS 012773 | 79 | 439 ± 25 | 69 – 122 | 96 |
| **SM10** | D-AMS 019434 | 34 | 104 ± 25 | -1 – 7 | 3 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | D-AMS 019436 | 58 | 449 | ± | 28 | 84 | – | 163 | 118 |
| | D-AMS 019437 | 63 | 384 | ± | 29 | 103 | – | 138 | 141 |
| | D-AMS 019438 | 70 | 479 | ± | 26 | 130 | – | 228 | 177 |
| | D-AMS 022098 | 88 | 593 | ± | 61 | 225 | – | 334 | 275 |
| | D-AMS 022099 | 110 | 740 | ± | 34 | 348 | – | 462 | 406 |
| | D-AMS 022100 | 124 | 970 | ± | 45 | 434 | – | 551 | 495 |
| | D-AMS 022102 | 152 | 1063 | ± | 43 | 588 | – | 740 | 658 |
| **SM15** | D-AMS 019444 | 50 | 610 | ± | 24 | 89 | – | 242 | 152 |
| | D-AMS 012774 | 55 | 573 | ± | 23 | 126 | – | 305 | 208 |
| | UBA-32342 | 75 | 1732 | ± | 32 | 752 | – | 1154 | 997 |
| | D-AMS 019445 | 78 | 1508 | ± | 29 | 899 | – | 1169 | 1045 |
| | D-AMS 012775 | 89 | 1583 | ± | 23 | 1058 | – | 1269 | 1163 |
| | D-AMS 012776 | 104 | 2447 | ± | 32 | 1269 | – | 1703 | 1478 |
| | D-AMS 029627 | 120 | 2106 | ± | 29 | 1482 | – | 1845 | 1665 |
| | D-AMS 029628 | 135 | 1556 | ± | 29 | 1634 | – | 2098 | 1830 |
| **SM25** | D-AMS 019439 | 8 | 216 | ± | 46 | -50 | – | 64 | 7 |
| | D-AMS 014000 | 28 | 508 | ± | 20 | 77 | – | 243 | 165 |
| | D-AMS 019440 | 35 | 608 | ± | 27 | 144 | – | 303 | 229 |
| | D-AMS 014001 | 39 | 604 | ± | 29 | 181 | – | 383 | 272 |
| | D-AMS 012777 | 49 | 1000 | ± | 27 | 427 | – | 637 | 538 |
| | D-AMS 019441 | 56 | 1234 | ± | 27 | 628 | – | 852 | 728 |
| | D-AMS 012778 | 70 | 1957 | ± | 24 | 1170 | – | 1525 | 1375 |
| | D-AMS 019442 | 76 | 1985 | ± | 25 | 1428 | – | 1533 | 1532 |
| | D-AMS 012779 | 89 | 2178 | ± | 28 | 1619 | – | 1871 | 1749 |

**Table S3.** Infrared bands, related molecular bonds and biomolecules assigned in seagrass sediments.

| Inorganic Functional Groups | | | |
|---|---|---|---|
| **Wavenumber (cm$^{-1}$)** | **Bands assignments** | **Component** | **Ref.** |
| 423 | Silicate Si-O | Silicates | a, b |
| 469 | Silicate Si-O | Silicates | a, b |
| 531 | Silicate Si-O | Silicates | a, b |
| 672 | Hydroxyl O-H; Silicate Si-O | Silicates | a, b |
| 693 | Hydroxyl O-H; Silicate Si-O | Silicates | b |
| 711 | Hydroxyl O-H; Silicate Si-O; $CO_3^{-2}$ | Silicates, Carbonates (calcite) | b, c, d |
| 751 | Hydroxyl O-H; Silicate Si-O; Si-Si | Silicates | a, b |
| 777 | Hydroxyl O-H; Silicate Si-O | Silicates; Biogenic silica (Bsi) | b, e, f |
| 798 | Hydroxyl O-H; Silicate Si-O | Silicates; Biogenic silica (Bsi) | b, e, f |
| 855 | Hydroxyl O-H; Silicate Si-O; $CO_3^{-2}$ | Silicates, Carbonates | a, b, c, d |
| 874 | Hydroxyl O-H; Silicate Si-O; $CO_3^{-2}$ | Silicates, Carbonates | a, b, c, d |
| 906 | Hydroxyl O-H; Silicate Si-O | Silicates | a, b |
| 982 | Si-O | Silicates | a, b |
| 1004 | Si-O | Silicates | a, b |
| 1032 | Si-O | Silicates; Biogenic silica (Bsi) | a, b, e |
| 1060 | Si-O | Silicates; Biogenic silica (Bsi) | a, b, e |
| 1082 | Si-O | Silicates; Biogenic silica (Bsi) | a, b, e |
| 1112 | Si-O | Silicates; Biogenic silica (Bsi) | a, b, e, f |
| 1164 | Si-O | Silicates | a |
| 1401 | $CO_3^{-2}$ | Carbonates | a, b, c |
| 1410 | $CO_3^{-2}$ | Carbonates | a, b, c |
| 1416 | $CO_3^{-2}$ | Carbonates | a, b, c, d |
| 1448 | $CO_3^{-2}$ | Carbonates | a, b, c |
| 1478 | $CO_3^{-2}$ | Carbonates | a, b, c |
| 1511 | $CO_3^{-2}$ | Carbonates | a, b, c |
| 1653 | | | |
| 1688 | | | |
| 1794 | $CO_3^{-2}$ | Carbonates | c, d |
| 2286 | | | |
| 2322 | | | |
| 2348 | | | |
| 2380 | | | |
| 2521 | $CO_3^{-2}$ | Carbonates | c |
| 2845 | $CO_3^{-2}$ | Carbonates | d |
| 2881 | $CO_3^{-2}$ | Carbonates | c |
| 2902 | $CO_3^{-2}$ | Carbonates | c |
| 2922 | | | |
| 2937 | | | |
| 2955 | | | |
| 2985 | $CO_3^{-2}$ | Carbonates | c |
| 3004 | | | |
| 3023 | $CO_3^{-2}$ | Carbonates | c |
| 3399 | O–H stretching and bending | Silicates (clay minerals) | b |
| 3568 | O–H stretching and bending | Silicates (clay minerals) | b |

| | | | |
|---|---|---|---|
| 3619 | O–H stretching and bending | Silicates (clay minerals) | b |
| 3632 | O–H stretching and bending | Silicates (clay minerals) | b |
| 3650 | O–H stretching and bending | Silicates (clay minerals) | b |
| 3693 | O–H stretching and bending | Silicates (clay minerals) | b |

**Organic Functional Groups**

| Wavenumber (cm$^{-1}$) | Bands assignments | Component | Ref. |
|---|---|---|---|
| 423 | | | |
| 469 | | | |
| 531 | | | |
| 672 | CH out of plane bending | Aromatic compounds | g |
| 693 | CH out of plane bending | Aromatic compounds | g |
| 711 | CH out of plane bending | Aromatic compounds | g |
| 751 | CH out of plane bending | Aromatic compounds | g |
| 777 | CH out of plane bending | Aromatic compounds | g |
| 798 | CH out of plane bending | Polysaccharides; aromatic compounds | g, h |
| 855 | CH out of plane bending | Polysaccharides; aromatic compounds | g, h |
| 874 | C-H out of plane bending | Polysaccharides; aromatic compounds | g, h |
| 906 | C–O stretching; carbon ring | Polysaccharides; cycling compounds | h, i |
| 982 | C–O stretching | Polysaccharides. | h, i, j |
| 1004 | C–O stretching | Polysaccharides | h, i, j |
| 1032 | C–O stretching; CH-O-H in cyclic alcohols | Polysaccharides, phenolic compounds | h, i, j, k |
| 1060 | C–O stretching | Polysaccharides | h, i, j, l |
| 1082 | C–O stretching | Polysaccharides | h, i, j, l |
| 1112 | C–O stretching | Polysaccharides, phenolic compounds | h, i, j, k, l |
| 1164 | C-O stretching, OH stretching and P=O stretching | Polysaccharides; phenolic compounds | h, i, j, k, l, m |
| 1401 | C–H bending of CH$_2$ and CH$_3$ groups, COO− anti-symmetric stretching | Aliphatic chains of proteins, carbohydrates and lipids | j, l,n |
| 1410 | C–H bending of CH$_2$ and CH$_3$ groups, COO− anti-symmetric stretching | Aliphatic chains of proteins, carbohydrates and lipids | j, l, n |
| 1416 | O–H deformation and stretching of phenolic -OH and C-O, CH deformation of CH$_2$ and CH$_3$ | Phenolic and aliphatic groups | j, m, n |
| 1448 | CH asymmetric bending; N-N=O, C-N=O and -CS-NH-stretching; Aromatic C=C stretching within ring | Aliphatic chains of proteins, carbohydrates and lipids; Primary amides and proteins; aromatic hydrocarbons (cell wall polysaccharides), phenolic compounds | h, j, k, l, m, o |
| 1478 | N-N=O, C-N=O and -CS-NH-stretching; Aromatic C=C stretching within ring | Primary amides and proteins; aromatic hydrocarbons, phenolic compounds | h, j, k, m |
| 1511 | Aromatic C=C stretching; C=N stretching and N-H deformation (Amide II band) | Proteins, aromatic hydrocarbons, phenolic compounds | i, j, k, l, m, o |
| 1653 | C=O stretching (Amide I)<br>NH bending vibration (amide II band) | Proteins and pectins, phenolic compounds | h, i, j, k, l, m, p |

| | | | |
|---|---|---|---|
| 1688 | C=O stretching (Amide I) | Proteins and pectins | m |
| 1794 | Saturated ester C=O stretching | Phospholipids, cholesterol esters, hemicellulose, and pectin; ester fatty acids | l, o |
| 2286 | C-C and C-N triple bond; N=C=O | Isocyanate | |
| 2322 | C-C and C-N triple bond | $CO_2$, Amino-related component | |
| 2348 | C-C and C-N triple bond; C=N=O asymmetric stretch vibration. | $CO_2$, Amino-related component | |
| 2380 | C-C and C-N triple bond | $CO_2$, Amino-related component | |
| 2521 | O–H stretching | Carboxylic acid | q |
| 2845 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | h, i, j, l, m, p |
| 2881 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | j, l, m, p |
| 2902 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | h, j, l, m, p |
| 2922 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | h, i, j, l, m, p |
| 2937 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | j, l, m, p |
| 2955 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | i, j, l, m, p |
| 2985 | C-H stretching | Aliphatic compounds: Lipids, proteins and carbohydrates | i, m |
| 3004 | N–H and O–H stretching modes | Proteins and polysaccharides | i |
| 3023 | C–H stretching; N–H and O–H stretching modes | Unsaturated hydrocarbon chains; Polysaccharides and proteins | i, l |
| 3399 | O–H and N–H stretching modes | Polysaccharides, proteins and phenolic compounds | h, j, l, p |
| 3568 | O–H and N–H stretching modes | Polysaccharides and proteins | i |
| 3619 | O–H and N–H stretching modes | Polysaccharides and proteins | i |
| 3632 | O–H and N–H stretching modes | Polysaccharides and proteins | i |
| 3650 | O–H and N–H stretching modes | Polysaccharides and proteins | i |
| 3693 | O–H and N–H stretching modes | Polysaccharides and proteins | i |

[a]Matteson & Herron (1993). [b]Margenot *et al.* (2017). [c]Bruckman & Wriessnig (2012). [d]Tatzber et al. (2007). [e]Sacket et al. (2016). [f]Vogel et al. (2016). [g]Margoshes &Fassel (1955). [h]Benito-Gonzalez et al. (2019). [i]Wissel et al. (2008). [j]Giovanela et al. (2004). [k]Rengasamy (2011). [l]Mecozzi et al. (2009). [m]Plis et al. (2014). [n]Enev et al. (2014). [o]Gorgulu et al. (2007). [p]Villacorte et al. (2015). [q]Baes and Bloom (1989).

**Table S4**. Mean C and N elemental composition and stable isotopes of seagrass sediment organic matter located along the coast of Andalusia and in the Cabrera Island.

| Core | N | $\delta^{15}N$ | C | $\delta^{13}C$ | CN |
|---|---|---|---|---|---|
| **CA** | 0.10 ± 0.09 | 1.49 ± 1.15 | 2.58 ± 1.82 | -16.47 ± 4.56 | 37.00 ± 9.45 |
| **ME** | 0.13 ± 0.11 | 1.43 ± 0.86 | 1.87 ± 1.35 | -14.12 ± 1.59 | 28.26 ± 6.74 |
| **RO** | 0.10 ± 0.04 | 1.49 ± 0.66 | 3.88 ± 1.44 | -12.20 ± 0.77 | 59.16 ± 17.34 |
| **BA** | - | - | 0.23 ± 0.08 | -20.20 ± 0.83 | - |
| **AG** | 0.07 ± 0.03 | 2.90 ± 0.72 | 3.64 ± 1.56 | -15.39 ± 2.00 | 52.51 ± 11.56 |
| **DE** | 0.08 ± 0.01 | 3.07 ± 0.55 | 1.33 ± 0.51 | -17.36 ± 1.62 | 20.11 ± 5.74 |
| **TE** | 0.13 ± 0.06 | 1.56 ± 1.02 | 2.73 ± 2.00 | -14.07 ± 1.75 | 40.81 ± 16.14 |
| *Coast of Andalusia* | *0.09* ± *0.05* | *2.48* ± *0.99* | *2.01* ± *1.79* | *-15.64* ± *2.79* | *38.26* *20.12* |
| **SM05** | 0.05 ± 0.01 | 0.18 ± 1.57 | 2.91 ± 1.06 | -19.76 ± 1.54 | 70.33 ± 19.30 |
| **SM10** | 0.04 ± 0.03 | -2.01 ± 4.25 | 0.92 ± 0.56 | -20.04 ± 1.52 | 34.06 ± 9.17 |
| **SM15** | 0.04 ± 0.03 | 0.13 ± 2.65 | 1.32 ± 0.49 | -20.37 ± 1.36 | 39.83 ± 13.33 |
| **SM25** | 0.04 ± 0.01 | -0.18 ± 1.57 | 1.37 ± 0.26 | -22.41 ± 0.89 | 41.90 ± 8.03 |
| **SM bay** | 0.04 ± 0.023 | -0.66 ± 3.162 | 1.45 ± 0.878 | -20.65 ± 1.67 | 41.47 ± 14.36 |
| **EP** | 0.12 ± 0.03 | 1.82 ± 0.69 | 4.98 ± 1.45 | -22.58 ± 1.87 | 51.61 ± 8.64 |
| *Cabrera Island* | *0.06* ± *0.04* | *-0.18* ± *3.02* | *2.16* ± *1.74* | *-21.03* ± *1.88* | *43.53* ± *13.99* |

**Table S5**. Seagrass shoot densities in our study sites taken from the literature.

| Location | Depth | Shoot density (mean ± sd) | Sampling year(s) | Reference |
|---|---|---|---|---|
| Cabrera, EP Bay | 2 | 1019 ± 60 | 2000-2001 | Holmer et al. (2003) |
| | 5 | 307 ± 11 | 2000 | Marbà et al. (2002a) |
| | 7 | 538 ± 36 | 2004-2006 | Terrados et al. (2008) |
| | 17 | 245 ± 16 | 2004-2006 | Terrados et al. (2008) |
| Cabrera, SM Bay | 7 | 1000 ± 34 | 2000-2001 | Marbà et al. (2002b) |
| | 7 | 726 ± 48 | 2004-2006 | Terrados et al. (2008) |
| | 7 | 478 ± 154 | 2000 | Marbà et al. (2002a) |
| | 7 | 815 | 2002 | Marbà & Duarte (2010) |
| | 7 | 740 | 2003 | Marbà & Duarte (2010) |
| | 7 | 890 | 2004 | Marbà & Duarte (2010) |
| | 7 | 800 | 2006-7 | Marbà & Duarte (2010) |
| | 9.4 | 627 ± 89 | 2008 | Agència Balear de l'Aigua i de la Qualitat Ambiental (2011) |
| | 13 | 288 ± 51 | 2000-2001 | Holmer et al. (2003) |
| | 13 | 470 ± 37 | 2001-2013 | Mazarrasa et al. (2007b) |
| | 13 | 762 ± 31 | 2000-2001 | Marbà et al. (2002b) |
| | 13 | 288 ± 51 | 2000 | Marbà et al. (2002a) |
| | 13 | 600 | 2002 | Marbà & Duarte (2010) |
| | 13 | 525 | 2003 | Marbà & Duarte (2010) |
| | 13 | 475 | 2004 | Marbà & Duarte (2010) |
| | 13 | 410 | 2006-7 | Marbà & Duarte (2010) |
| | 17 | 461 | 2000-2001 | Marbà et al. (2002b) |
| | 17 | 312 ± 22 | 2004-2006 | Terrados et al. (2008) |
| | 17 | 440 | 2002 | Marbà & Duarte (2010) |
| | 17 | 375 | 2003 | Marbà & Duarte (2010) |
| | 17 | 360 | 2004 | Marbà & Duarte (2010) |
| | 17 | 355 | 2005 | Marbà & Duarte (2010) |
| | 17 | 280 | 2006-7 | Marbà & Duarte (2010) |
| | 18 | 287 ± 46 | 2000 | Marbà et al. (2002a) |
| | 26.5 | 187 ± 20 | 2000 | Marbà et al. (2002a) |
| Andalusia, TE | 10.6 | 386 ± 102 | 2013 | CAGDPS, 2018 |
| | 10.6 | 370 ± 78 | 2014 | CAGDPS, 2018 |
| | 10.6 | 286 ± 74 | 2016 | CAGDPS, 2018 |
| | 10.6 | 281 ± 84 | 2017 | CAGDPS, 2018 |
| | 10.6 | 272 ± 62 | 2018 | CAGDPS, 2018 |
| Andalusia, DE | 11 | 81 ± 21 | 2012 | CAGDPS, 2018 |
| | 13 | 65 ± 20 | 2013 | CAGDPS, 2018 |
| | 14 | 54 ± 21 | 2014 | CAGDPS, 2018 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Andalusia, AG | 13 | 199 | ± | 65 | 2012 | CAGDPS, 2018 |
| | 12 | 150 | ± | 50 | 2013 | CAGDPS, 2018 |
| | 12 | 118 | ± | 24 | 2014 | CAGDPS, 2018 |
| | 12 | 269 | ± | 78 | 2015 | CAGDPS, 2018 |
| | 12 | 242 | ± | 63 | 2016 | CAGDPS, 2018 |
| | 12 | 190 | ± | 30 | 2017 | CAGDPS, 2018 |
| | 12 | 133 | ± | 29 | 2018 | CAGDPS, 2018 |
| Andalusia, RO | 12 | 315 | ± | 86 | 2012 | CAGDPS, 2018 |
| | 11 | 366 | ± | 60 | 2013 | CAGDPS, 2018 |
| | 11 | 299 | ± | 46 | 2014 | CAGDPS, 2018 |
| | 11 | 264 | ± | 77 | 2015 | CAGDPS, 2018 |
| | 11 | 228 | ± | 82 | 2016 | CAGDPS, 2018 |
| | 11 | 226 | ± | 48 | 2017 | CAGDPS, 2018 |
| | 11 | 133 | ± | 29 | 2018 | CAGDPS, 2018 |
| Andalusia, ME | 7.5 | 404 | ± | 106 | 2010 | CAGDPS, 2018 |
| | 7.5 | 405 | ± | 100 | 2011 | CAGDPS, 2018 |
| | 7.5 | 457 | ± | 81 | 2013 | CAGDPS, 2018 |
| | 7.5 | 545 | ± | 138 | 2014 | CAGDPS, 2018 |
| | 7.5 | 798 | ± | 91 | 2015 | CAGDPS, 2018 |
| | 7.5 | 404 | ± | 90 | 2017 | CAGDPS, 2018 |
| | 7.5 | 545 | ± | 96 | 2018 | CAGDPS, 2018 |
| Andalusia, CA | 3 | 65 | ± | 12 | 2004 | CAGDPS, 2018 |
| | 3 | 168 | ± | 13 | 2010 | CAGDPS, 2018 |
| | 2.5 | 89 | ± | 17 | 2011 | CAGDPS, 2018 |
| | 3 | 134 | ± | 32 | 2012 | CAGDPS, 2018 |
| | 3 | 139 | ± | 16 | 2013 | CAGDPS, 2018 |
| | 3.4 | 105 | ± | 23 | 2014 | CAGDPS, 2018 |
| | 4 | 263 | ± | 20 | 2015 | CAGDPS, 2018 |
| | 3 | 308 | ± | 56 | 2017 | CAGDPS, 2018 |
| | 3 | 193 | ± | 34 | 2018 | CAGDPS, 2018 |

# APPENDIX D

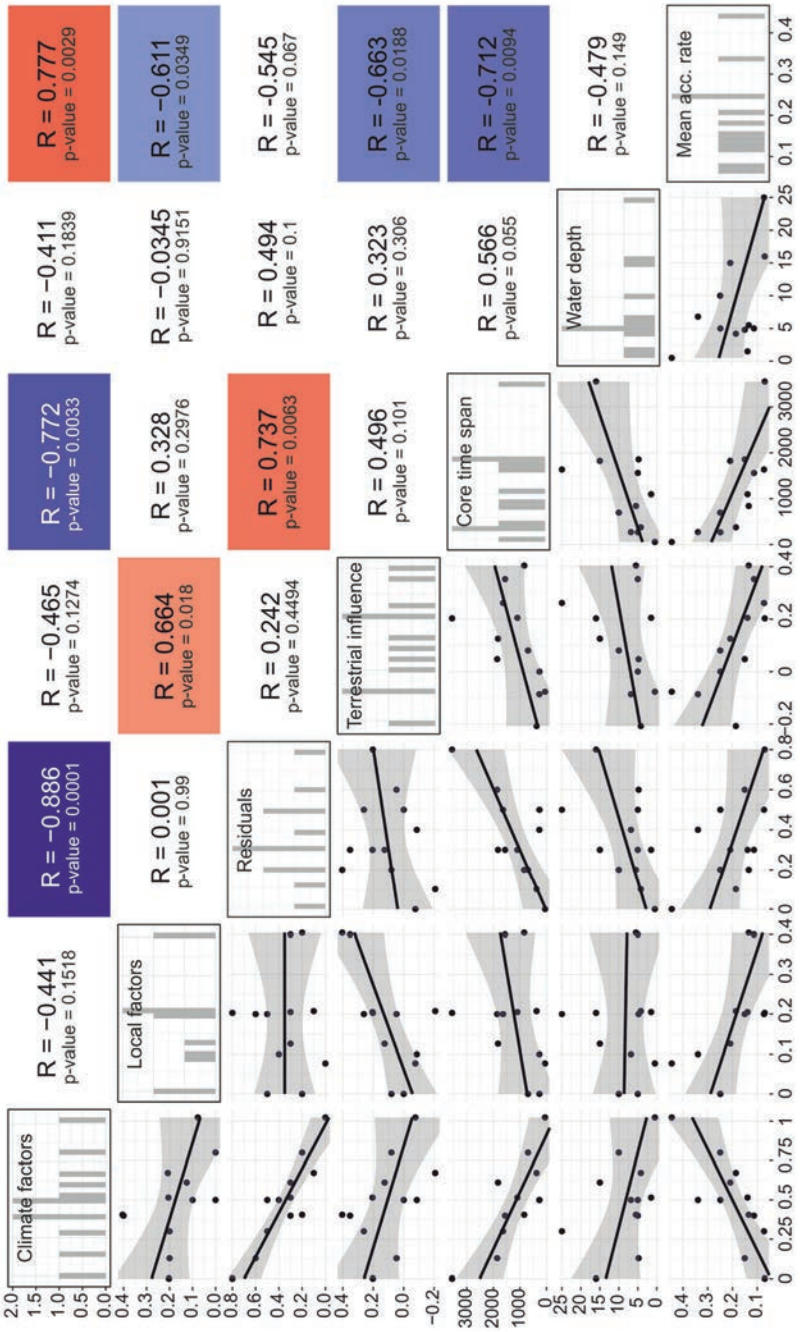
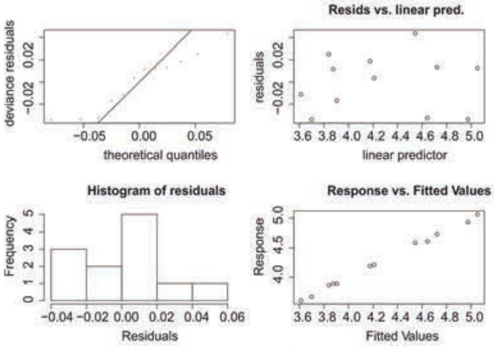
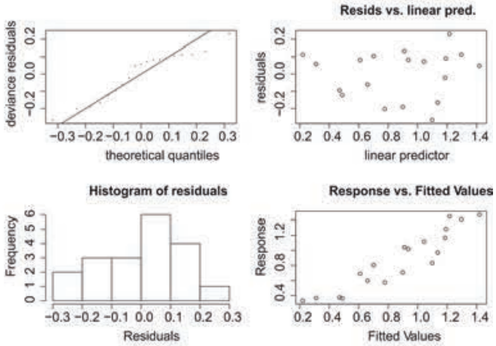


**Figure S7.** Linear Pearson correlations between explained deviance of model terms (grouped in global climatic factors, local factors, residuals and terrestrial influence) and encompassed time period, water depth and mean sediment accumulation rate (cm/y).

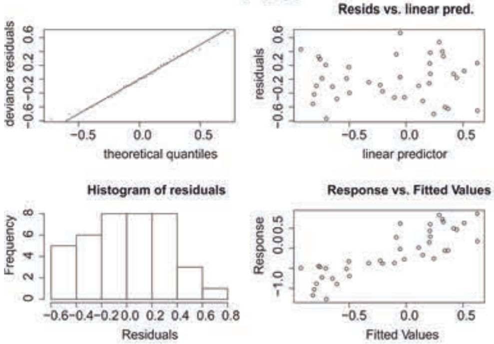
CA



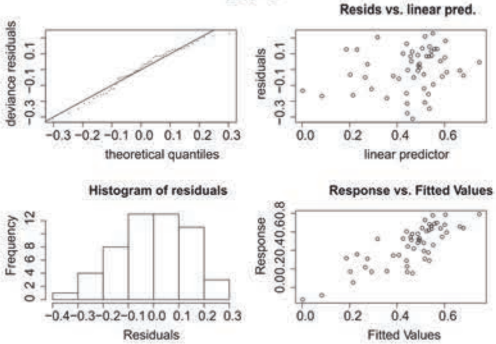
ME



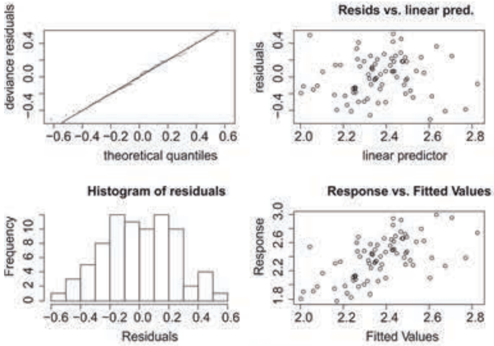
RO



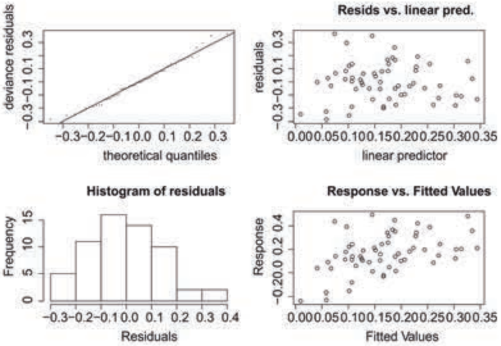
BA



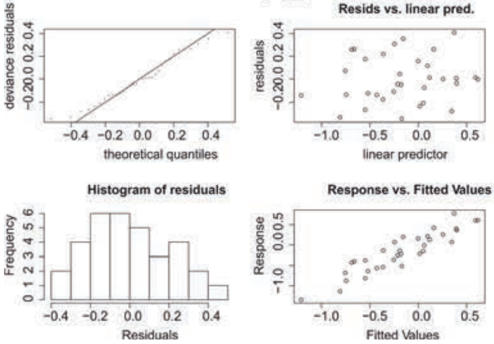
AG



DE



TE



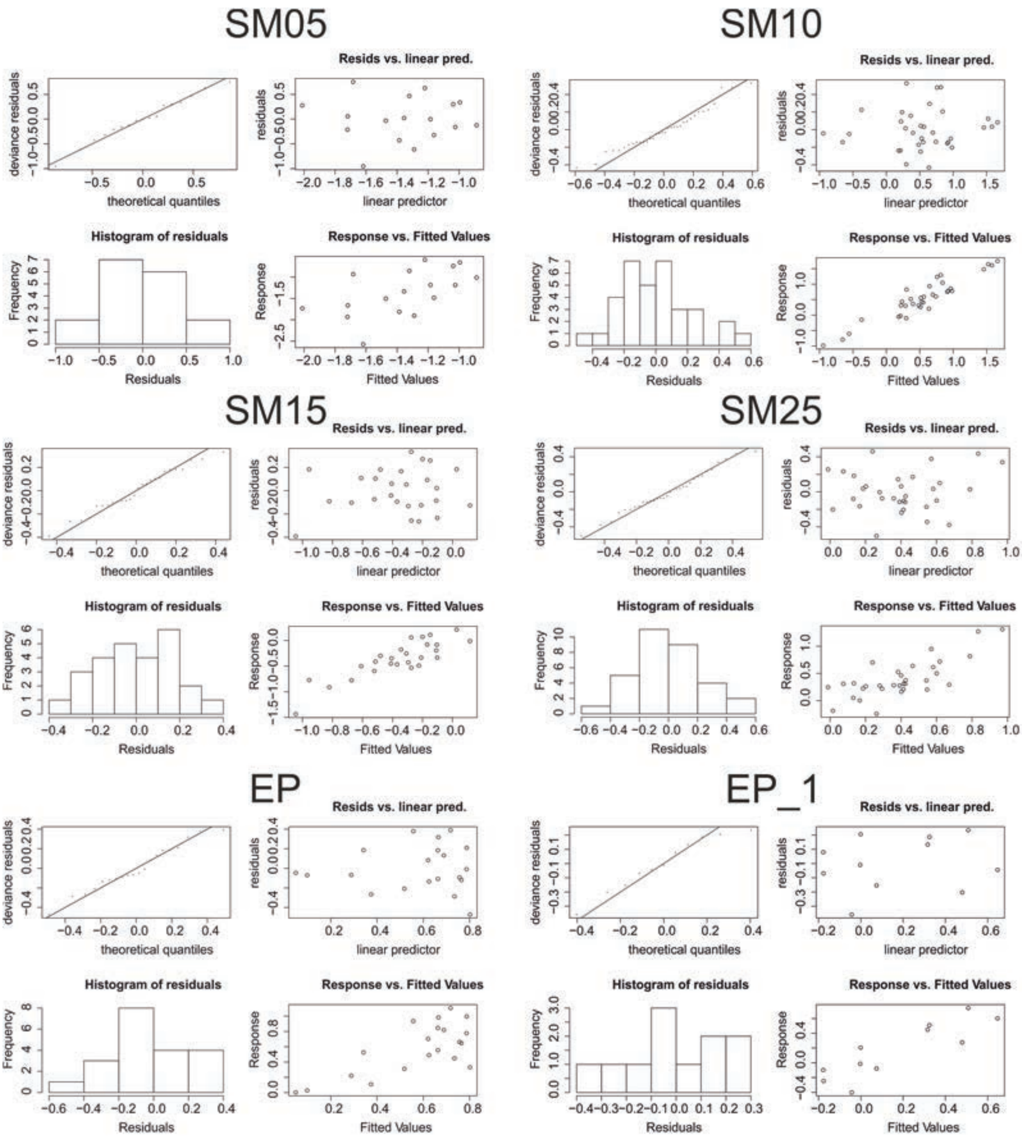


**Figure S8.** Validation plots for each core GAM model. It includes QQ-plots and histograms, used to assess normality; residuals versus fitted values to assess homogeneity and the response versus fitted values, to evaluate the model fit and which should ideally show a *straight line*.

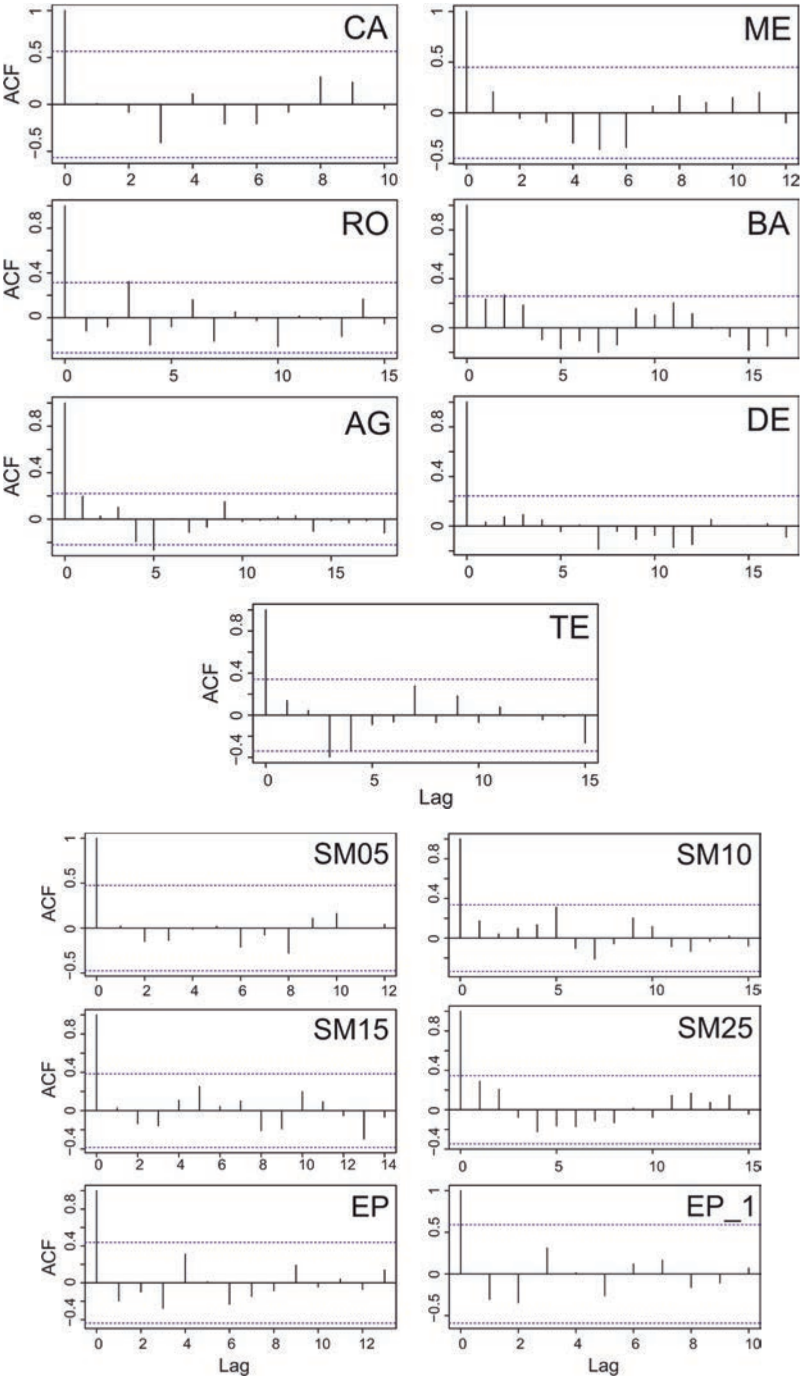


**Figure S9.** Plots of autocorrelation function (ACF) of the residuals from each core GAM model, used to check if there is any structure left in the residuals. The blue dashed lines represent the confidence interval lines with a 95% coverage probability.

# PUBLISHED ARTICLES

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Reasearh article

# Millennial-scale trends and controls in *Posidonia oceanica* (L. Delile) ecosystem productivity

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ABSTRACT

*Posidonia oceanica* is a marine phanerogam that buries a significant part of its belowground production forming an organic bioconstruction known as mat. Despite *Posidonia* seagrass mats have proven to be reliable archives of long-term environmental change, palaeoecological studies using seagrass archives are still scarce. Here we reconstruct four millennia of environmental dynamics in the NE coast of Spain by analysing the carbon and nitrogen stable isotopic composition of *P. oceanica* sheaths, the proportion of different seagrass organs throughout the seagrass mat and other sedimentological proxies. The palaeoenvironmental reconstruction informs on long-term ecosystem productivity and nutrient loading, which have been linked to global (e.g., solar radiation) and local (e.g., land-use changes) factors. The long-term environmental records obtained are compared with previous palaeoecological records obtained for the area, showing a common environmental history. First, a relative seagrass ecosystem stability at ~4000 and 2000 cal. yr BP. Then, after a productivity peak at ~1400–800 cal. yr BP, productivity shows an abrupt decline to unprecedented low values. The fluctuations in ecosystem productivity are likely explained by increases in nutrient inputs related to human activities – mostly in the bay watershed – concomitantly with changes in total solar radiation. Cumulative anthropogenic stressors after Roman times may have started to affect ecosystem resilience, dynamics and productivity, with more abrupt regime shifts during the last millennium. These results add into recent research showing the potential of seagrass archives in reconstructing environmental change and seagrass post-disturbance dynamics, hence providing unvaluable information for improving the efficiency in managing these key coastal ecosystems.

## 1. Introduction

Seagrass meadows provide unvaluable ecosystem services, as they constitute biodiversity hotspots, improve the quality of coastal waters, stabilize sediments and reduce shoreline erosion (Duarte, 2002). However, they are declining worldwide due to anthropogenic pressures, including global change (Short and Neckles, 1999; Orth et al., 2006). In recent times, substantial efforts have been invested to preserve seagrass meadows, key in current European environmental policies. *Posidonia* meadows are protected as a priority habitat (Council Directives, 1992, 1997), as a species (Bern Convention, 1979; Barcelona Convention, 1976), under specific legal protection actions in individual countries (e.g., Albania, Croatia, France, Italy, Spain and Turkey), and included in marine protected areas along the Mediterranean Sea (UNEP-MAP-RAC/SPA, 2009). Monitoring programs are taken place since the end of the 20th century, such as the Posidonia Monitoring Network in the Provence-Alpes-Côte d'Azur region (PACA) in France, or the POSIMED project along the Mediterranean coast of Spain.

However, monitoring programs present several handicaps, including the limited time-span they cover (i.e., short-term environmental records). Ecosystem dynamics occur at multiple spatiotemporal scales, and the discrimination of centennial and millennial patterns and processes needs an adequate time perspective (Seddon et al., 2014). Therefore, long-term environmental records are a priority. In this sense, a palaeoecological approach provides long-term environmental records. The longer time span they cover enables the reconstruction of pre-anthropogenic scenarios, the discrimination between natural and human-induced perturbations, and the determination of regime shifts as well as

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the ecosystems' resilience to perturbations (e.g., Willard and Cronin, 2007; Benton and Harper, 2009; Davies and Bunting, 2010; López-Merino et al., 2012). Regime shifts are abrupt changes on several trophic levels leading to fast ecosystem reconfiguration, usually after abrupt climatic changes or anthropogenic impacts (Andersen et al., 2009). Knowing the relevant long-term processes resulting in abrupt ecological changes provides priceless information for guiding ecosystem conservation strategies (Willis et al., 2005, 2007; Davies and Bunting, 2010; Birks, 2012).

*P. oceanica* shows seasonal dynamics in productivity with shoot growth peaking in late summer and declining in fall (Alcoverro et al., 1995, 1997). This annual pattern is mainly regulated by changes in light and water temperature associated with solar insolation (Alcoverro et al., 1995, 1997). Moreover, a feedback control on growth is caused due to seasonal variability in resources and local conditions generated by the seagrass growth. *P. oceanica* growth is controlled by light and temperature in winter, while in summer it is limited by nutrients (Alcoverro et al., 1997). Considering this information, on a centennial to millennial scale it would be expected a productivity pattern regulated by solar irradiance if no other limiting resource or disturbance occurred. Local factors (e.g., nutrients, carbon, redox potential, physical processes) play a major role in growth as limiting factors in meadows with high light availability (Pérez and Romero, 1992; Alcoverro et al., 1995, 1997), especially nutrient availability (Romero et al., 2006). Disturbances may cause deviations from the observed seasonal pattern caused by solar irradiance (Short and Wyllie-Echeverria, 1996). On the one hand, natural disturbances are extreme climatic events, changes in wave exposure and tidal currents, diseases, grazing and bioturbation. On the other hand, human-induced disturbances are eutrophication, dredging, filling and certain fishing practices causing direct physical damage (Short and Wyllie-Echeverria, 1996).

Environmental archives are especially scarce in marine coastal areas owing to high hydrodynamic energy and bioturbation (Mateo et al., 2010). However, *P. oceanica*, a slow-growing and climax seagrass species, amongst the most productive of all marine ecosystems (Duarte, 1991a; Mateo et al., 2006), forms coherent sedimentary sequences with temporal resolution ranging from 2 to 17 $\mathrm{yr\,cm^{-1}}$ (Serrano et al., 2016a).

*P. oceanica* is composed by rhizomes, leaf shoots and roots. The leaves proximal end presents a cylindrical structure known as leaf sheath, attached to the rhizome. The high lignin and phenolic content of the seagrass debris confers them a remarkable decay-resistant nature (Kaal et al., 2016). The annual accumulation of the refractory fraction of the *P. oceanica* organic debris, together with the accumulation of other organic and inorganic particles trapped in the meadow, results in a bioconstruction known as mat (or "matte"; Boudouresque and Meinesz, 1982), consisting in massive pools of organic matter (OM) sequestered over millennia and with a thickness reaching up to 6.5 m (Mateo et al., 1997; Lo Iacono et al., 2008; Pergent et al., 2012). The anoxic conditions prevailing in the mat favour the preservation of abiotic and biotic proxies (Mateo et al., 1997, 2006), thus enabling the application of a palaeoecological approach on the *P. oceanica* archive (e.g., López-Sáez et al., 2009; Mateo et al., 2010; Serrano et al., 2011, 2013, 2016b, 2016c; López-Merino et al., 2015, 2017; Kaal et al., 2016).

Soils under *P. oceanica* meadows are usually mixed siliciclastic–carbonate, the carbonate fraction mainly derived from epiphytic carbonate production and the great diversity of calcifying organisms that require the seagrass as shelter, source of food and substrate (Mateu-Vicens et al., 2012; Gaglianone et al., 2017). The main control on the relative abundance of calcareous epiphytes is seagrass biomass. Mature and longer leaves with higher surface area host more epiphytes than the young ones and meadows with higher shoot densities and canopies host more calcifying organisms (Mazarrasa et al., 2015). Moreover, calcification within the meadow is enhanced with the increase of seawater pH due to the photosynthetic activity of the seagrass (e.g. Semesi et al., 2009). Following these premises, the carbonate content in the mat under the meadow could be a proxy of the seagrass productivity. However, if the geological substrate of the bay watershed is dominated by limestone, the carbonate content would not allow the discrimination between the biogenic production and the terrestrial input (Gaglianone et al., 2017).

Despite successful applications of stable isotope ratios in paleoceanography (Koch, 1998; Hayes et al., 1999), their potential to reconstruct changes in seagrass ecosystems remains largely unexplored. The stable isotope composition of plant tissues changes in response to environmental variability (Amundson et al., 2003; Mateo et al., 2004; Cernusak et al., 2013). Positive correlations between stable carbon isotopes ($\delta^{13}C$), solar irradiance and productivity have been reported for *P. oceanica*, opening the possibility of using $\delta^{13}C$ as a proxy for past changes in seagrass productivity, or even in solar irradiance if no other abrupt environmental disturbances occurred (Hemminga and Mateo, 1996; Mateo et al., 2000, 2010).

Nitrogen stable isotopes ($\delta^{15}N$) are more difficult to interpret due to their inherent variability (Fogel and Tuross, 1999). Different processes may influence the N isotope composition in aquatic plants. First, the isotopic signature of available N sources is highly variable (Gaye-Haake et al., 2005). Second, isotopic fractionation during nitrate and ammonium assimilation leads to post-assimilation changes in $\delta^{15}N$ values (Fogel and Cifuentes, 1993; Teranes and Bernasconi, 2000). Finally, bacterial degradation can also lead to a depleted isotopic signal in the residual organic matter during early diagenesis under anoxic conditions (Lehmann et al., 2002). Despite of this variability, $\delta^{15}N$ in aquatic plants has been used to discriminate between external N sources, mainly related to human disturbance (Chappuis et al., 2017).

In this study, we have applied a multi-proxy palaeoecological approach on a four-thousand-year-old *P. oceanica* mat located at the Portligat Bay in NE Spain. We have analysed for the first time biological proxies such as the proportions of sheath-, root- and rhizome-derived debris as well as the C and N elemental and isotopic composition of *P. oceanica* sheaths with the overarching aim of reconstructing the meadow productivity dynamics in order to reveal possible ecological regime shifts and the environmental drivers behind them.

## 2. Study area

The Portlligat Bay (Cap de Creus Natural Park, NE Spain) is a small and shallow inlet (0.14 $\mathrm{km^2}$ and < 10 m deep) connected to the sea by a 213 m opening to the NE. It is a sheltered bay, protected from winds and sea storms. A large part of the bay (41%) is covered by a meadow of *P. oceanica* with an average thickness of ~4.5 m alternating with sandy bioclastic patches (Lo Iacono et al., 2008). The meadow shows a strong phosporus deficiency (Alcoverro et al., 1995, 1997). There is not a permanent stream providing volumetrically important terrestrial inputs. The latter are instead modulated by run-off and by eventual strong discharges of a torrent, a seasonally active creek flowing into the bay from its NW shore (Fig. 1a).

The climate of the area is Mediterranean xeroteric (Franquesa i Codinach, 1995). The annual precipitation ranges between 200 and 1300 mm and mainly occurs from October to December (average range for 1950–2016, Servei Meteorològic de Catalunya). The bedrock geology of the catchment is mostly composed of phyllites, slates, schists and some quartzites and marbles which date from the Paleozoic (Cartographic Institute of Catalonia, 1997). > 50% of the watershed area has very steep slopes (> 60%). Soils are poorly developed, very shallow, fast draining and coarse textured. They have a 0.3% of carbonate and 1.8–4.3% of organic matter contents (Cartographic Institute of Catalonia, 2006).

Mediterranean shrubland dominates the current landscape. It mainly comprises *Cistus monspeliensis* L., *Cistus albidus* L., *Lavandula stoechas* L., *Calicotome spinosa* (L.), *Ulex parviflorus* Pourr, *Pistacia lentiscus* L., *Juniperus oxycedrus* L., *Arbutus unedo* L., *Quercus coccifera* L.

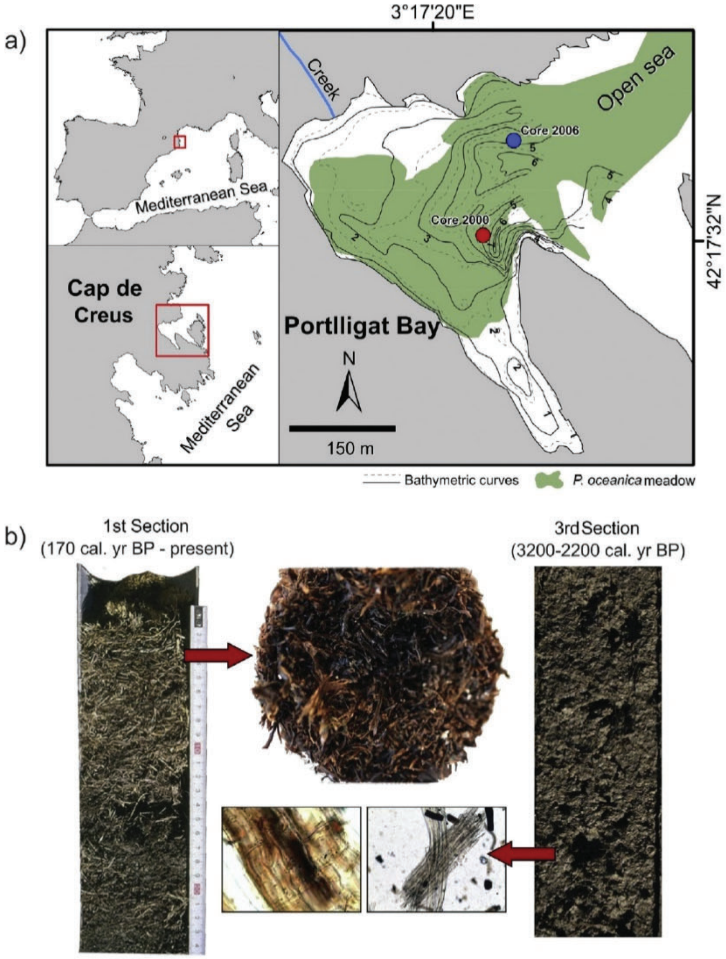


**Fig. 1.** (a) Location of the study area and the coring site of Core 2000 (red dot, this study) and Core 2006 (blue dot, López-Merino et al., 2017) (Portlligat Bay, Girona, Spain). (b) Core 2000 shows a dense matte with abundant organic matter for the first forty centimeters, changing to sands (fine to coarse size) with rhizomes, roots and leaf sheaths more degraded in deeper sections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and *Erica arborea* L. Forest cover is sparse, with small areas covered by cork oak trees (*Quercus suber* L.) and pines (*Pinus halepensis* Miller, *Pinus pinea* L.), while *Quercus ilex* L. and *Quercus pubescens* Willd. occur in sheltered areas (Franquesa i Codinach, 1995). The current landscape has been influenced by a long history of human activities, mostly related to farming (Franquesa i Codinach, 1995; López-Sáez et al., 2009, 2015, 2017). However, traditional dry-land farming and fisheries have recently been replaced by tourism, resulting in the abandonment of terraced vineyards (*Vitis vinifera* L.) and pasturelands.

## 3. Material and methods

### 3.1. Coring procedures and laboratory analyses

A 475-cm long core of *P. oceanica* mat was obtained in 2000 CE (Core 2000 from now on) from the Portlligat Bay at a depth of ~3 m (42° 17′32″ N; 3° 17′28″ E; Fig. 1a). It was recovered using a floating drilling platform with a self-powered drill, which combined percussion and rotation (see details in Serrano et al., 2012). The stratigraphy showed a dense mat with abundant organic matter for the first forty centimeters, changing to sands (fine to coarse size) with rhizomes, roots and leaf sheaths embedded within the sediment matrix below this depth (Fig. 1b).The core was sliced into 1 cm-thick slices and 176 samples were selected for the analyses. The samples were dried at 70 °C in order to calculate dry bulk density. Soil organic matter < 1 mm (SOM) was determined by loss-on-ignition (450 °C for 5 h) after dry-sievieng (1 mm) bulk subsamples. Total carbonate content ($CaCO_3$) was measured in bulk subsamples using a Scheibler calcimeter.

Subsamples were wet-sieved in seawater into two fractions, a coarse (> 1 mm) and a fine (1 mm ≥ fine > 63 μm) fraction. The coarse fraction was sorted into organic (coarse organic matter, COM, > 1 mm) and inorganic fractions. The organic fraction of COM was composed of rhizomes, leaf sheaths and roots, which were separated to account for their biomass. All fractions were dried at 70 °C until constant weight.

Elemental and isotopic C and N composition of *P. oceanica* sheaths were obtained using a Finnigan Delta S isotope ratio mass spectrometer 196 (Conflo II interface). Carbon and nitrogen isotope ratios are expressed as δ values in parts per thousand (‰) relative to the Vienna PeeDee Belemnite and atmospheric $N_2$ (air) standards, respectively. Analytical precision based on the standard deviation of internal standards ranged from 0.11 to 0.06‰.

After wet digestion of the *P. oceanica* sheaths, phosphorus content was measured at the Serveis Científico-Técnics, Barcelona University, using a JobinYvon JI-38 (3600 grooves $mm^{-1}$) ICP-AES following Mateo and Sabaté (1993).

Grain size distribution was determined using a Retsch AS 200 analytical sieve shaker for 15 min after wet-sieving (1 mm and 0.063 mm mesh) with distilled water and removing the COM only. Grain sizes were classified as gravel (> 2 mm), coarse sand (2–0.5 mm), medium sand (0.5–0.25 mm), fine sand (0.25–0.063 mm) and mud (silt and clay, < 0.063 mm), according to Brown and McLachland (1990).

The carbon and nitrogen stable isotopes, nitrogen and phosporus content of *P. oceanica* sheaths are original data for this paper, while the other data used were first published in Serrano et al. (2012).

### 3.2. Age-depth model

Serrano et al. (2012) presented an age-depth model for Core 2000 using a smooth-spline model. Here, we used Bacon.R software (Blaauw and Christen, 2011) and the same radiocarbon dates (Table 1). However, while Serrano et al. (2012) discarded two of the fourteen radiocarbon dates, we included them in the model so that the Bacon software could decide whether those radiocarbon dates should be consider outliers. They were finally not discarded. Moreover, we also included the age of the surface of the core, which is the year of recovery (2000 CE, Fig. 2). Radiocarbon dates are expressed as calibrated years before present. Dates were calibrated using the marine 13.14C calibration curve (Reimer et al., 2013) and a local marine reservoir correction was applied (ΔR = 23 ± 71 years, Siani et al., 2000).

### 3.3. Numerical exploration

The dataset used for the numerical analyses comprises 176 samples and 16 variables. These variables include: SOM, COM, $CaCO_3$, $\delta^{13}C$, $\delta^{15}N$, carbon, nitrogen and phosphorus contents in sheath remains, sheath debris biomass percentages, root debris biomass percentages, rhizome debris biomass percentages and five sediment grain-size fractions (Fig. 3).

Bulk density, accreation rates, $CaCO_3$, SOM and COM contents were used to estimate mass accumulation rates (MAR) of carbonates and organic matter, following Zachos et al. (2004). MAR are used rather than weight/weight percentages as they better express fluxes (e.g., delivery and preservation). Percentages are influenced by the closed nature of their calculation and, therefore, subjected to dilution/concentration effects (Meyers and Lallier-Vergès, 1999).

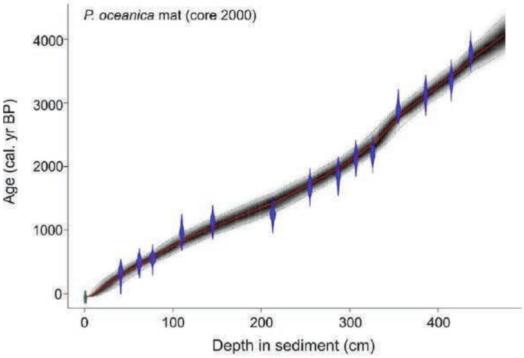


**Fig. 2.** Age-depth model of Core 2000 using Bacon.R software (Blaauw and Christen, 2011). Fourteen radiocarbon dates were calibrated using the marine13 radiocarbon age calibration curve (Reimer et al., 2013) and corrected for a local marine reservoir effect (ΔR = 23 ± 71 years, Siani et al., 2000). The red dashed curve shows the "best" model based on the weighted mean age for each depth. Individual radiocarbon dates are shown in probability density functions of calibrated ages. The grey area indicates the uncertainty envelope of the age model with grey dashed curves indicating 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

After data for each variable were transformed and standardized by substracting its mean and dividing by its standard deviation, we applied a series of numerical analyses using R software (R Development Core Team, 2011) and CPQtR1.0.3 (Gallagher et al., 2011) in order to detect common trends, main changes, and evaluate the influence of selected factors on the palaeoenvironmental history of the seagrass meadow of the last 4000 years.

Compositional data (granulometric distribution, elemental composition of sheath and organs biomass percentages) were transformed by centered log-ratio (Aitchinson, 1986), while Box-cox transformation method (Box and Cox, 1964) was applied to SOM MAR, COM MAR (λ = 0), and $CaCO_3$ MAR, $\delta^{13}C$, $\delta^{15}N$ in plant debris (λ = 1).

Principal component analysis (PCA) was applied to the variables dataset using the correlation matrix with a varimax rotation, determining the number of significant principal components (PC) with Parallel Analysis (Horn, 1965).

**Table 1**
Radiocarbon dates in the *P. oceanica* mat sediment Core 2000. The marine13.14C calibration curve was used for calibration and a local marine reservoir effect included (Delta $R = 23 \pm 71$ yr). Radiocarbon dates are taken from Serrano et al. (2011).

| Laboratory code | Material type | Depth (cm) | AMS $^{14}C$ date (yr BP) | Cal. yr BP (2σ range) | Weighted mean age |
|---|---|---|---|---|---|
| OS-29665 | *P. oceanica* sheaths | 41 | 710 ± 45 | 160 – 400 | 289 |
| OS-29666 | *P. oceanica* sheaths | 62 | 895 ± 45 | 343 – 555 | 461 |
| OS-29667 | *P. oceanica* sheaths | 77 | 975 ± 40 | 468 – 666 | 569 |
| OS-29668 | *P. oceanica* sheaths | 110 | 1430 ± 40 | 697 – 955 | 823 |
| OS-29651 | *P. oceanica* sheaths | 145 | 1600 ± 45 | 913 – 1181 | 1045 |
| OS-44491 | *P. oceanica* sheaths | 213 | 1710 ± 25 | 1269 – 1581 | 1425 |
| OS-44492 | *P. oceanica* sheaths | 255 | 2120 ± 30 | 1572 – 1871 | 1721 |
| OS-44493 | *P. oceanica* sheaths | 287 | 2270 ± 30 | 1821 – 2119 | 1967 |
| OS-44494 | *P. oceanica* sheaths | 307 | 2500 ± 30 | 2005 – 2304 | 2152 |
| OS-44497 | *P. oceanica* sheaths | 326 | 2560 ± 25 | 2184 – 2542 | 2345 |
| OS-44498 | *P. oceanica* sheaths | 355 | 3130 ± 25 | 2570 – 2934 | 2771 |
| OS-44499 | *P. oceanica* sheaths | 386 | 3320 ± 30 | 2947 – 3272 | 3111 |
| OS-44502 | *P. oceanica* sheaths | 415 | 3500 ± 35 | 3236 – 3576 | 3406 |
| OS-44504 | *P. oceanica* sheaths | 437 | 3850 ± 30 | 3473 – 3852 | 3663 |

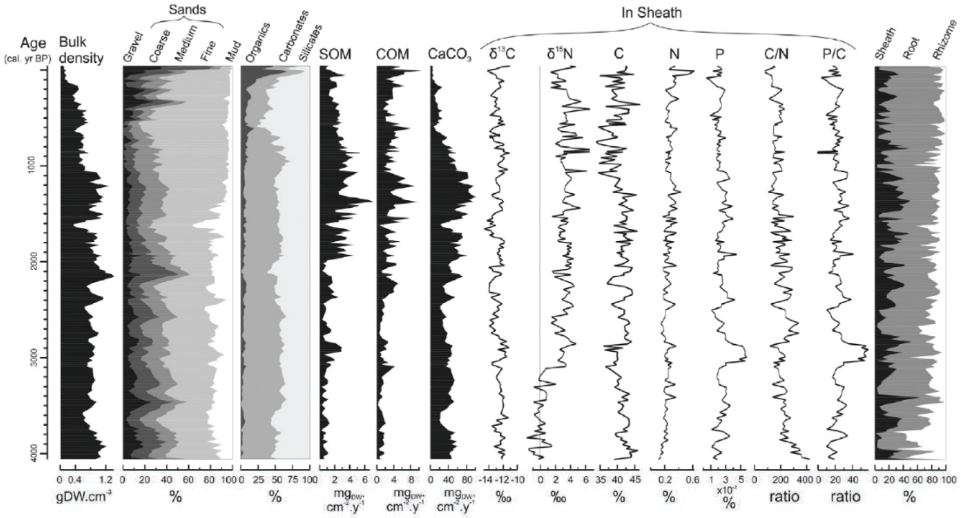


**Fig. 3.** Descriptive variables: changes in bulk density, sediment organic matter (SOM), coarse organic matter (COM) and carbonate content, $\delta^{13}$C, $\delta^{15}$N, C, N, P, C/N, C/P, organ debris distribution and grain size distribution along the *P. oceanica* mat sediment Core 2000 plotted against age. The percentage of organics is the sum of SOM (< 1 mm) and COM (> 1 mm) (i.e., the total organic matter content). Silicates correspond to the percentage of non-carbonate inorganic sediments. Organic matter and carbonate contents are also expressed as MAR (see text for explanation). Stable isotopes and elemental composition were analysed in the sheath debris.

Change-point modelling was applied to all records of PC scores together using a Bayesian transdimensional Markov chain Monte Carlo approach in order to identify common shifts in the trends obtained after the PCA. This approach infers probability distributions for the number and locations in time of changepoints and the mean values between changepoints on several trends (Gallagher et al., 2011).

Using partial redundancy analysis (pRDA), the PC scores were used as 'composite' response variables on which the influence of climate and anthropogenic activity was tested. Five pRDA models were run, one per PC, so one of the PC was the response variable in each of them. All models had the same four explanatory variables. Two explanatory variables were chosen to assess the influence of global climate patterns: Total Solar Irradiance (TSI, Steinhilber et al., 2012) and Northern Hemisphere temperature anomalies (NH temperature, Kobashi et al., 2013). The other two explanatory variables were selected to assess the influence of local factors. They are two records of heavy metals obtained after the PCA of the geochemical composition in sheaths in Core 2000 by Serrano et al. (2011). One record is related to heavy metals derived from anthropogenic activities (PC1m), likely linked to increased soil erosion in the catchment, while the other integrates metals with a more lithogenic and hence, natural geogenic origin (PC2m). All statistically significant pRDA models ($p < .05$) had sample ages partialled out as a covariable. It is important to partial out the statistical effects of age because of the strong temporal auto-correlation, a common feature of time series (Legendre et al., 2002). Most inferential statistical tests assume that residuals are independently and identically distributed, assumption violated if residuals are autocorrelated. Ignoring autocorrelation can result in false inferences. Monte Carlo permutation tests were used to test the significance of the model and of each predictor variable (999 permutations), obtaining the partial explained variation and the significance for every explanatory variable.

Additionally, Lomb-Scargle periodograms – especifically for unevenly sampled times series – were performed to detect statistically relevant periodicities present in the records of PC scores. All data were detrended by linear regression prior to analysis.

## 4. Results

### 4.1. Age-depth model and accretion rates

According to the age-depth model (Fig. 2), the Core 2000 dated back to 4000 cal. yr BP with accretion rates ranging from 0.7 to 1.7 mm yr$^{-1}$ (mean = 1.2 ± 0.3 mm yr$^{-1}$) and an average resolution of 8.8 ± 2.4 yr cm$^{-1}$. The 1–295 cm section (~2000–0 cal. yr BP) showed higher accretion rates (mean = 1.4 ± 0.2 mm yr$^{-1}$) than the 295–475 cm section (~4000–2000 cal. yr BP) (mean = 0.9 ± 0.1 mm yr¯1, Mann-Whitney U, two-tailed $p < .001$).

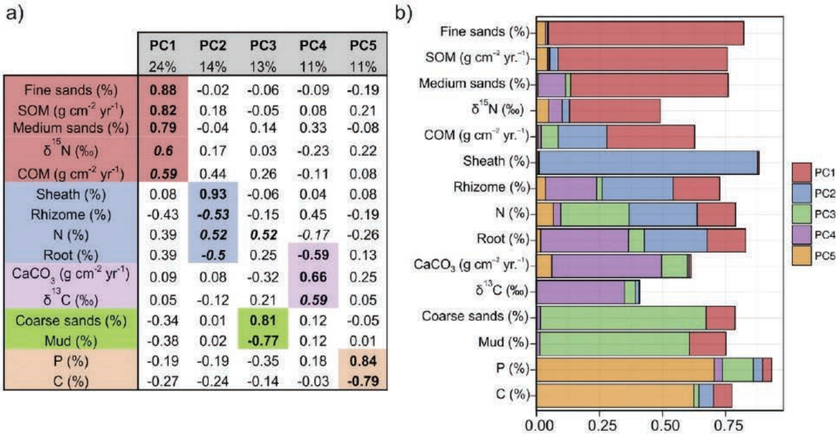
### 4.2. Principal component analysis and change point modelling

Five principal components explain 73% of the variance (Fig. 4). The first principal component (PC1) accounts for 24% of the variance, showing positive loadings for SOM MAR, COM MAR, $\delta^{15}$N and medium and fine sands. The second principal component (PC2) explains 14% of the variance, showing negative loadings for root and rhizome biomass and positive loadings for sheath biomass and nitrogen in sheath. The third principal component (PC3) explains 13% of the variance, showing positive loadings for coarse sands and N in sheath and a negative loading for mud. The fourth principal component (PC4) explains 11% of the variance, showing positive loadings for CaCO$_3$ MAR and $\delta^{13}$C and a negative loading for root biomass. Finally, the fifth principal component (PC5) explains 11% of the variance, showing a positive loading for P in sheath and a negative loading for C in sheath.

The change-point modelling applied to the five records of PC scores suggests 12 statistically significant regime shifts (change-points CP-1 to CP-12; Fig. 5). Four of them (CP-3, CP-4, CP-7 and CP-8) at the scale of centuries, while the rest are more abrupt, occurring within decades. CP-6, CP-9, CP-11 and CP-12 are the most abrupt regime shits.

### 4.3. Influence of explanatory variables

pRDA models for the records of PC scores were all statistically significant ($p = .001$) except for PC2 (Fig. 6; Table 1 of Supplementary



a)

| | PC1<br>24% | PC2<br>14% | PC3<br>13% | PC4<br>11% | PC5<br>11% |
|---|---|---|---|---|---|
| Fine sands (%) | **0.88** | -0.02 | -0.06 | -0.09 | -0.19 |
| SOM (g cm$^{-2}$ yr$^{-1}$) | **0.82** | 0.18 | -0.05 | 0.08 | 0.21 |
| Medium sands (%) | **0.79** | -0.04 | 0.14 | 0.33 | -0.08 |
| $\delta^{15}N$ (‰) | ***0.6*** | 0.17 | 0.03 | -0.23 | 0.22 |
| COM (g cm$^{-2}$ yr$^{-1}$) | ***0.59*** | 0.44 | 0.26 | -0.11 | 0.08 |
| Sheath (%) | 0.08 | **0.93** | -0.06 | 0.04 | 0.08 |
| Rhizome (%) | -0.43 | ***-0.53*** | -0.15 | 0.45 | -0.19 |
| N (%) | 0.39 | ***0.52*** | ***0.52*** | *-0.17* | -0.26 |
| Root (%) | 0.39 | ***-0.5*** | 0.25 | **-0.59** | 0.13 |
| CaCO$_3$ (g cm$^{-2}$ yr$^{-1}$) | 0.09 | 0.08 | -0.32 | **0.66** | 0.25 |
| $\delta^{13}C$ (‰) | 0.05 | -0.12 | 0.21 | ***0.59*** | 0.05 |
| Coarse sands (%) | -0.34 | 0.01 | **0.81** | 0.12 | -0.05 |
| Mud (%) | -0.38 | 0.02 | **-0.77** | 0.12 | 0.01 |
| P (%) | -0.19 | -0.19 | -0.35 | 0.18 | **0.84** |
| C (%) | -0.27 | -0.24 | -0.14 | -0.03 | **-0.79** |

**Fig. 4.** (a) Factor loadings of the descriptive variables of Core 2000 used in the PCA. Numbers in bold indicate variables with factor loadings > 0.6 and in bold italics are those with moderate factor loadings (0.5 to 0.6). The individual percentage of variance explained is given under each factor. Factor loadings represent correlation coefficients between the variables and the principal components. (b) Communalities. The communality accounts for the proportion of each variable's variance explained by the five extracted principal components. The total length of the bars is the communality of each element, while the sections represent the proportion of variance allocated in each individual principal component.

material), and they explained from 15 to 36% of the variance of the response variables.

On the one hand, the variance explained by the pRDA model for PC1 as a composite variable was the lowest (15.3%), PC1m composite variable being the main predictor followed by TSI and its interaction with NH temperature (Fig. 6; Table 1 of Supplementary material). On the other hand, the variance explained for PC3 as a composite variable was the largest (36%). Again, PC1m composite variable explained the largest proportion of variance, followed by TSI. Other second-degree interactions between climatic variables and PC1m composite variable contributed to explain up to 11% of variance. For PC4-composite variable, climatic variables explained 6.5% (comprising TSI, NH temperature and their interaction), quite similar to the 6.9% explained by local factors (PC1m and PC2m composite variables). A contribution of

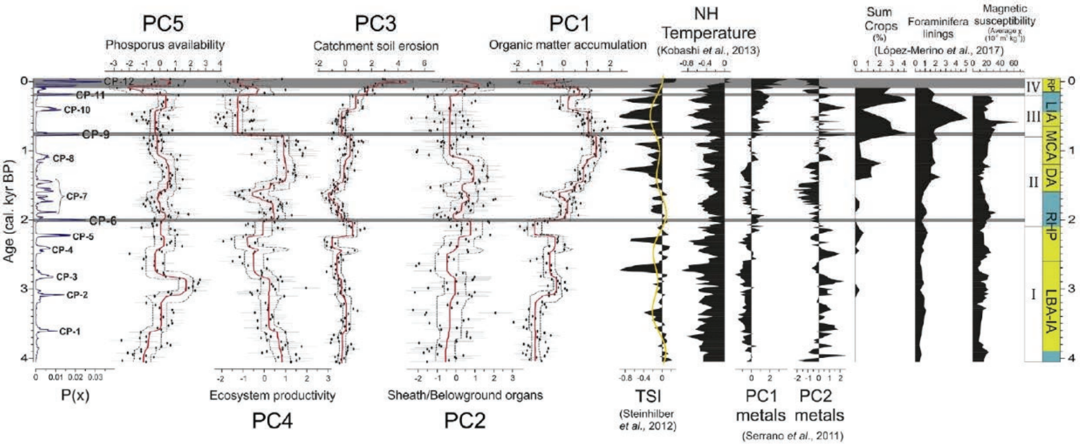


**Fig. 5.** Long-term ecological dynamics detected in the *P. oceanica* meadow of Portlligat Bay. Black dots correspond to the original data and horizontal lines are the noise estimation, which is the standard deviation of the unknown error (normal) distribution for a given data set. Thick red curves represent the average after 100,000 functions, while grey lines define 95% confidence interval ranges. The blue curve on the left shows the probability of the change-point [P(x)]. PC: Principal component, CP: Change Point. Horizontal grey bands highlight abrupt regime shifts with high probability.The change point functions are compared to Total Solar Irradiance (TSI), given as difference in W/m$^2$ to the value of the PMOD composite during the solar cycle minimum of the 1986 CE (1365.57 W/m$^2$; Steinhilber et al., 2012); Northern Hemisphere (NH) temperature, given as anomalies (°C) from 1961–1990 CE (Kobashi et al., 2013); PC1m, considered to be related to anthropogenic activities in the catchment, and PC2m, related to metals with a lithogenic origin (Serrano et al., 2011); sum of crops (Cerealia-t., *Cannabis/Humulus*-t., *Juglans*, *Castanea* and *Vitis*) is a palynological indicator of land-use change; foraminifera linings account for eutrophication of the bay waters and magnetic susceptibility indicates changes in the seagrass mat organic/inorganic content. Sum of crops, foraminifera linings and magnetic susceptiblity data are from Core 2006, a core obtained 150 m apart from Core 2000 (López-Merino et al., 2017). On the right, the four phases identified in this study are indicated as well as arid (yellow) and humid (blue) phases (Pérez-Sanz et al., 2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

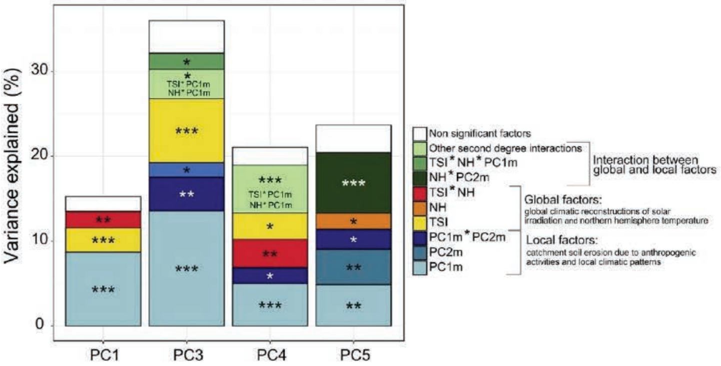


**Fig. 6.** Percentage of partial explained variation and significance of individual terms (explanatory variables) assesed using Monte Carlo permutation tests (999 permutations, levels of significance: $*p \leq .05$, $**p \leq .01$, $***p \leq .001$.) in every partial RDA.

5.6% by the interactions between local and large-scale factors was also found. The predictor which explained a higher proportion of PC5-composite variable was the interaction between NH temperature and PC2m composite variable (7.1%) followed by the record of PC1m (4.9%).

### 4.4. Spectral analysis

PC3 and PC4 present comparable cycles with periodicities of ~1000 yr (1100 and 970 yr, respectively), while PC1 and PC5 show similar cycles with wavelenghts centered at ~2000 yr (2060 and 1710 yr, respectively; Fig. 7). Moreover, PC4 presents a significant periodicity at 2500 yr, as well as one close to significance at 520 yr (Fig. 7). There was not any significant cycle observed for PC2.

## 5. Discussion

### 5.1. Trends in the P. oceanica long-term ecosystem dynamics

PC1 seems to indicate changes in organic matter (OM) accumulation and diagenesis (Fig. 4; COM MAR and SOM MAR positive loadings). PC1 positive scores reflect a higher accumulation and lower degree of degradation of OM in the upper section of the mat (Fig. 5; i.e., top ~250 cm, since ~1700 cal. yr BP). The decrease of the score values

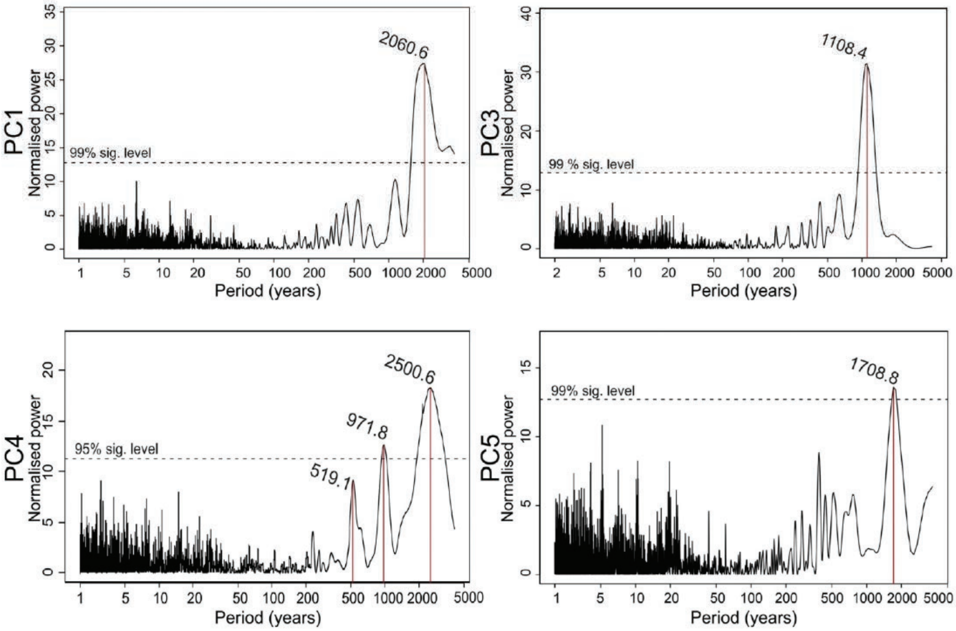


**Fig. 7.** Lomb-Scargle normalized periodograms (spectral power as a function of periodicity) of principal components PC1, PC3, PC4 and PC5. The horizontal dotted line marks the significance level. Prominent periodicities are indicated with red lines. There was not any significant cycle observed for PC2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with depth would be partially related to OM decomposition. $\delta^{15}N$ of sheath debris also shows a positive loading (Fig. 4), most likely linked to a better preserved OM, generally enriched in the heavy isotope (Möbius et al., 2010). In the case of *P. oceanica*,Fourqurean and Schrlau (2003) and unpublished data of project SUMAR (CTM2006–12492/MAR) reported that $\delta^{15}N$ values decreased substantially during decomposition. The positive loadings that medium and fine sands also show (Fig. 4) are problably related to the fact that the OM < 1 mm was not digested prior the granulometric analysis and it may predominate in the fine fractions (< 1 mm), at least in the upper part of the core. Hence, these sands are mostly corresponding to that OM fraction. The changes observed in the OM accumulation indicated by PC1 scores seem to be mainly explained by anthropogenic activities (PC1m) and secondarely by TSI (Fig. 6; Table 1 in Supplementary material). The anthropogenic metal pollution record (PC1m) could be used as an indicator of general human impact, whose main consequence in coastal areas is catchment soil erosion (López-Merino et al., 2017). Changes in catchment soil erosion rates can have a large effect in sediment inputs into the bay and, hence, in the availability of nutrients and oxygen in the seagrass soils, factors known to be key drivers for the decay rates of *P. oceanica* and other aquatic angiosperms remains (Godshalk and Wetzel, 1978a, 1978b; Mateo and Romero, 1996). Climatic variables exert an inherent control on ecosystem productivity (e.g., effect of irradiance and temperature in photosynthesis), likely affecting the OM supply to the soil.

The positive loading of sheath biomass and negative loadings of root and rhizome (i.e., belowground) biomass in PC2 (Fig. 4) suggest a link with the availability of nutrients in the column water for the plant. PC2 positive scores indicate higher amounts of sheath biomass in comparison with the belowground biomass. The negative relationship between the sheath and the belowground biomass would indicate changes in the allocation of plant biomass, which in seagrasses is related with changes in nutrient concentration change (McGlathery, 2008). The shoot:root ratio increases with high-nutrient availability, while with low-nutrient conditions seagrasses allocate biomass to belowground tissues in order to increase the surface area for nutrient uptake (Powell et al., 1989; Vogt et al., 1993; Pérez et al., 1991, 1994, 2001; Nixon et al., 2001). Furthermore, N in sheath debris also shows a positive loading (Fig. 4), another indicator of higher nutrient availability since N content in tissues increases with higher N availability (e.g., Pérez et al., 2008).

PC3 scores record accounts for the opposite distribution of coarse sands (positive loading) and mud (negative loading) (Fig. 4), likely recording changes in soil erosion. Soil erosion affecting the granulometry of seagrass soils could have different drivers. One driver could be climate, as Mediterranean climate is characterised by sporadic torrential floods resulting in transport of coarser sediments (e.g., Walling et al., 2000; Roca et al., 2009). Land-use change in the catchment could also drive changes in the grain size distribution of the seagrass soils, as it could trigger soil erosion (López-Merino et al., 2017). Coarser fractions in seagrass soils could also be explained by higher local hydrodinamism in the meadow. Higher hydrodynamism (e.g., due to riverflow or runoff waters) causes resuspension and removal of the mud fraction. In fact, PC3 is mostly influenced by anthropogenic activities triggering catchment soil erosion (PC1m) followed by TSI (Figs. 6 and 8; Table 1 in Supplementary material). TSI controls atmospheric and rainfall patterns that also affect catchment soil erosion.

PC4 relates key variables linked to the productivity of the ecosystem. $CaCO_3$ MAR and $\delta^{13}C$ show positive loadings versus the negative loading of root biomass. Carbonates content in seagrasses is consistent with bio-calcification in seagrass meadows and the meadow overall productivity (e.g., Gacia et al., 2003; Semesi et al., 2009). The continental origin of carbonates is less likely than the biogenic source since the phyllosilicate minerals dominate the catchment geology of the Portlligat Bay. The positive loading of $\delta^{13}C$ of sheath would agree with the known positive correlation between $\delta^{13}C$ and seagrass productivity (Hemminga and Mateo, 1996; Mateo et al., 2000). The negative loading of root content fits in the overall picture, as the allocation of biomass to belowground tissue is reduced with high nutrient availability and, hence, productivity (Powell et al., 1989; Pérez et al., 1991, 1994, 2001). PC4 is influenced by anthropogenic activities, as shown by the PC1m record (Fig. 6; Table 1 in Supplementary material). Human impact would be associated with enhanced soil erosion and, therefore, nutrient input. Higher inputs of nutrients and trace metals, such as iron, may stimulate seagrass productivity and sheath biomass production (Marbà et al., 2007; Udy and Dennison, 1997; Lee and Dunton, 2000). NH temperature and TSI climatic variables also affect PC4 (Fig. 6; Table 1 in Supplementary material), consistent with the positive effect of temperature and irradiance on seagrass productivity (Duarte, 1991b; Pérez and Romero, 1992; Ruiz and Romero, 2001; Nejrup and Pedersen, 2008; Marbà and Duarte, 2009; Mateo et al., 2010; Gacia et al., 2012).

PC5 contrasts P and C contents in sheath, likely linked with the P:C ratio, a known proxy for phosporus availability in seagrasses (e.g., Duarte, 1990). When the plant is strongly limited by P, its tissues are depleted in this nutrient relative to C content, so the P:C ratio would be lower. As nutrient availability increases plant tissues become enriched in P relative to the C content, resulting in increasing P:C ratios (Duarte, 1990). PC5 is mainly affected by local factors (PC1m and PC2m), as they influence soil erosion in the watershed which largely controls the delivery of nutrients into the bay (Fig. 6; Table 1 in Supplementary material).

The variance explained by pRDA models ranged from 15.3 to 36%, evidencing that a substantial part of the principal components variability is unexplained by the chosen global and local predictors (Fig. 6; Table 1 in Supplementary material). Other factors that could have played an important role controlling seagrass ecosystem dynamics for the last ~4000 years are local changes in water transparency or temperature – as they can enhance sulphide stress (García et al., 2012) –, dissolved inorganic C availability (Invers et al., 1999, 2001), competition with other primary producers and soil bacteria (e.g., López et al., 1998; Dumay et al., 2002; Alcoverro et al., 2004), or herbivory (e.g., Tomas et al., 2005).

The spectral analysis showed that soil erosion and productivity (PC3 and PC4) share a periodicity of ~1000 yr; while OM accumulation and P availability (PC1 and PC5) share a periodicity of ~2000 yr. Other

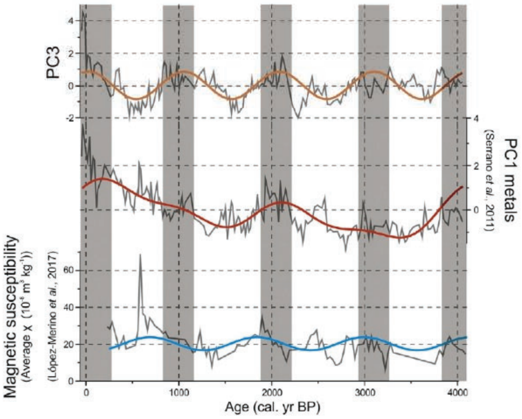


**Fig. 8.** Sum of sinusoids fits using periods from Lomb-Scargle periodograms, showing ~1000 years cycles for the soil erosion record (PC3, this study); periods ~4000, ~2000 and ~1000 years cycles for PC1m (Serrano et al., 2011) and period ~1100 for magnetic susceptibility (López-Merino et al., 2017). Vertical grey bands highlight phases of high soil erosion which co-occur with high anthropogenic pressure (PC1m) and high terrestrial inputs (magnetic susceptiblity).

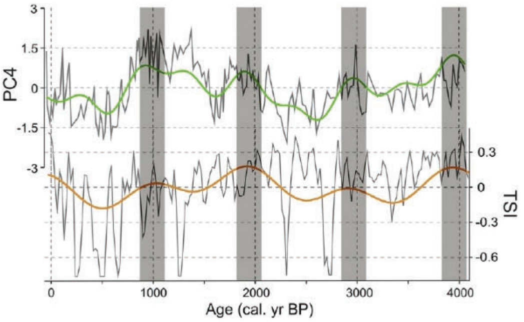


**Fig. 9.** Sum of sinusoids fits using periods from Lomb-Scargle periodograms, showing ~520, ~970 and ~2500 years cycles for the productivity record (PC4) and ~980 and ~2300 years cycles for the Total Solar Irradiance series (Steinhilber et al., 2012). Vertical grey bands highlight phases of solar irradiance maximum, which co-occur with productivity maximum.

periodicities, only linked to productivity (PC4), are 520 and 2500 yr (Fig. 7). Although periodicities may be affected by non-climatic factors (e.g., internal seagrass dynamics), analogous cycles do appear in power spectra of solar activity reconstructions: a ~500 yr cycle, the Eddy cycle (~1000 yr) and the Hallstatt cycle (~2000 yr) (Yin et al., 2007; Dima and Lohmann, 2008; Steinhilber et al., 2012).The 2500 yr cycle could be a fingerprint of the Hallstat cycle, as Yin et al. (2007) observed that its ranges from 2040 to 2400 yr. Therefore, the spectral analysis and the pRDA results provide evidence to support the effect of TSI in the seagrass ecosystem trends.

The productivity record (PC4) is the only one presenting the three cycles. TSI and productivity trends follow a similar pattern, with intervals of increased TSI associated with increased productivity at ~1000, 2000, 3000 and 4000 cal. yr BP (Fig. 9). Terrestrial ecosystems functioning and photosynthesis depend on downward solar radiation at the Earth's surface (Sinclair et al., 1976; Medvigy et al., 2010). An analogous pattern is followed by *P. oceanica* ecosystems, suggesting that the productivity of underwater vegetation is also sensitive to changes in TSI (Fig. 9. However, even if the detected periodicities are driven by solar cycles, they could also be affected by autogenic mechanisms, subsampling resolution, or a combination of the two factors (Turner et al., 2016).

### *5.2. Limitations of using $\delta^{13}$C measured in P. oceanica sheath debris as a proxy of productivity*

A larger positive loading of $\delta^{13}$C of plant tissues in the productivity component (PC4) was expected, coherent with the relationships between $\delta^{13}$C of plant tissues, leaf net production and irradiance found by Mateo et al. (2000, 2010) in field observations and experiments. $\delta^{13}$C in plant tissues (and derived detritus) responds to changes in the trade-off between C availability and demand, related to light and temperature variations. The long-term ecological results obtained in our work suggest that other factors are superimposed to changes in $\delta^{13}$C values.

One factor that could affect $\delta^{13}$C of plant tissues is meadow depth, as the correlation with production and irradiance is weaker in shallow meadows, as in Portlligat, than in those growing closer to the compensation irradiance (Mateo et al., 2000). Assuming no significant changes in sea level for the last four millennia in the area (Vacchi et al., 2016), the depth at which the meadow was growing 4000 years ago would have been around 7 m (3 m water depth at present plus 4 m mat thickness; Lo Iacono et al., 2008). A lower irradiance would have resulted in a lower photosynthetic demand and a higher discrimination against the heavy isotope. Following this rationale, the $\delta^{13}$C of ancient seagrasses debris should have been more negative than more recent debris. However, no evident trend is found, indicating that this effect is not as important as other factors. Another factor that could affect $\delta^{13}$C of plant tissues is that the shape of the transfer functions found for the reconstructions was that of a saturation curve (Mateo et al., 2010). This means that resolution of changes in $\delta^{13}$C at higher productivity levels is lower and consequently changes might not be properly paralleled by the proxy, making the values at the higher end less accurate. Hence, small changes in the $\delta^{13}$C record would be more meaningful than they seem to be.

The preservation of $\delta^{13}$C in plant tissues exposed to diagenetic processes is still a long-standing matter of controversy (Wu et al., 2003; Wang et al., 2008; Alewell et al., 2011), questioning its potential as palaeoecological proxy. Microbial reworking of OM during early diagenesis can modify its bulk carbon isotopic content (Meyers and Lallier-Vergès, 1999; Boström et al., 2007). However, there is no clear trend in the literature. According to Meyers and Lallier-Vergès (1999) the overall diagenetic isotope shift in OM isotopic composition in Lake Michigan is minimal, ~1–2‰ shifts towards less negative $\delta^{13}$C values. Wang et al. (2008) observed differences in $\delta^{13}$C of up to 2.8‰ between vegetation and bottom organic matter. Fourqurean and Schrlau (2003) observed a steady decline in $\delta^{13}$C of the seagrass *Thalassia testudinum* leaves during decomposition over the course of a year, so that leaves detritus became depleted in $^{13}$C by ~2‰. This could indicate that variations in underwater soil conditions (e.g., higher nutrient inputs that could increase soil anoxia) could vary the diagenetic effect on $\delta^{13}$C of the detritus and, hence, blur the correlation between $\delta^{13}$C in sheaths with TSI and plant production. Preliminary results from in situ degradation experiments of *P. oceanica* sheaths in anoxic conditions (buried at around 10 cm in the sediment), showed no significant changes in $\delta^{13}$C over 277 days (Project SUMAR, CTM2006-12492/MAR, unpublished data). Although this is an important finding to support the adequacy of $\delta^{13}$C for palaeoenvironmental reconstruction, the effect of diagenesis over much longer periods of time remains untested and, therefore, further work is required to validate $\delta^{13}$C signatures of *P. oceanica* tissues as a proxy of productivity.

### *5.3. Chronology of the environmental and ecological changes*

Four phases are distinguished according to the main regimen shifts identified by change point modelling (CP-12, CP-11, CP-9 and CP-6; Fig. 5).

#### *5.3.1. Phase I: Two millennia of relative stability with a steady decline in productivity (~4000–2000 cal. yr BP)*

The records of PC scores showed lower values and variability from ~4000 to 2000 cal. yr BP. The productivity record (PC4) presents high scores at ~4000 cal. yr BP, following a decreasing trend until ~2000 cal. yr BP. The lower scores of the OM accumulation record (PC1) and the record of nutrient availability (PC2) are in accordance with the decreasing trend in ecosystem productivity. This period is described as arid in the Portlligat Bay owing to the abundance of *Pinus* and evergreen *Quercus* as well as in other Iberian records by the expansion of *Pinus*, sclerophyllous and/or steppe taxa (López-Merino et al., 2017 and references therein). The arid conditions occur in the context of a decline in TSI (Fig. 5; Steinhilber et al., 2012).

The first half of Phase I (~4000–3400 cal. yr BP), shows low impact of anthropogenic activities in the area, as indicated by other studies (Fig. 5; Riera-Mora and Esteban-Amat, 1994; López-Merino et al., 2017), suggesting low nutrient supply to the marine environment from soil erosion. The onset of agriculture practices in the catchment is observed by palynological analysis at ~3400–2900 cal. yr BP (López-Merino et al., 2017). Anthropogenic impact steadily increased after ~3400 cal. yr BP, peaking at ~2600–2400 cal. yr BP with an increase in metal pollution due to mining and a larger importance of agriculture (Fig. 5; Serrano et al., 2011; López-Merino et al., 2017).

Overall, Phase I shows a decreasing trend in TSI and an increasing trend in anthropogenic pressure, but still low human impact on the coastal environment. Light seems to have been the main limiting factor for productivity. The strong decline in TSI likely overrided the effect in production derived from higher nutrient availability.

#### 5.3.2. *Phase II: Higher productivity and variability (~2000–800 cal. yr BP)*

Throughout this phase the records of most principal components show higher scores, although with higher variance. Phase II starts with two abrupt changes: CP-5 and CP-6, both taking place during Roman times. An important increase in the coarser sediment fraction, sheath:belowground ratio and productivity are recorded between CP-5 and CP-6. Coarser sediments, along with increased productivity and nutrient inputs, could be explained by the conjuction of more intense human activities (i.e., mining and agriculture) in the catchment during Roman times (Serrano et al., 2011; López-Merino et al., 2017) and to enhanced flooding in eastern Iberia between ~2450 and 2150 cal. yr BP (Benito et al., 2015). Seagrass meadows in Portlligat Bay may have been nutrient-limited; hence anthropogenic- and climate-induced terrigenous inputs would have increased the concentration of nutrients resulting in a higher productivity and a lower allocation of resources to belowground tissues.

The record of scores of all principal components reach a minimum at ~1600 cal. yr BP, when crops decreased in the catchment (Fig. 5; López-Merino et al., 2017). Croping resumed at the onset of the Visigothic period at ~1500 cal. yr BP (Fig. 5; López-Merino et al., 2017). Productivity, sheath:belowground ratio and P availability increased during the Visigothic period, the first two reaching some of the highest values recorded. Therefore, the seagrass productivity at the bay recovered previous levels of production. The end of the Visigothic period is synchronous with another major regime shift, CP-8 (~1400–1050 cal. yr BP). Phosphorus availability and sheath:belowground ratio decrease, while productivity remains constant. The reduction in nutrient supply following the decrease in the agricultural activity at the end of the Visigothic period (López-Sáez et al., 2009; López-Merino et al., 2015, 2017) had no impact on the productivity of the ecosystem. Higher values in TSI could be behind this trend (Fig. 5).

Phase II shows high, constant TSI values, as well as increased nutrient inputs, linked to higher human impact. Despite this, during this phase there is an abrupt change in productivity at ~1600 cal. yr BP coeval with lower evidence of human activities, the overall trend indicates that the seagrass growth over Phase II is regulated by nutrient availability.

#### 5.3.3. *Phase III: Abrupt decline in productivity: Crossing an ecological threshold? (~800–200 cal. yr BP)*

An abrupt change in productivity took place at ~800 cal. yr BP (CP-9). The region experienced an increase in crops at ~800–600 cal. yr BP, that is reflected in the higher magnetic susceptibility (i.e., soil erosion) of the seagrass mat and in the abundance of foraminifera linings (i.e., eutrophication) as detected in the nearby Core 2006 (Fig. 5; López-Merino et al., 2017). These changes are consistent with rapid deforestation in the area (Riera-Mora and Esteban-Amat, 1994; López-Sáez et al., 2009; López-Merino et al., 2015, 2017). During this chronological interval, TSI exhibits several minima (Figs. 5 and 8), within the context of the Little Ice Age, a climatic anomaly driven by a decline in summer insolation (Mayewski et al., 2004; Steinhilber et al., 2012; Oliva et al., 2018). The combination of low TSI with increasing human impact might have impacted the dynamics of *Posidonia* meadows through diverse and complex mechanisms. First, an excess of sediment and nutrient loadings entering the bay may derive in a poor light environment reinforced by the low TSI, as well as in an increased sediment anoxia (Rabalais and Turner, 2001). Second, decreased carbohydrates reserves which are crucial to survive during periods of low TSI (when C balance can be negative) could have compromised the seagrass growth. These decreases in carbohydrates reserves have been observed in the field following nutrient increases, since N assimilation requires energy and C skeletons, resources obtained from the carbohydrate reserves (Invers et al., 2004; Alcoverro et al., 2001). The overall ecosystem resilience seems to have crossed a threshold, causing the sudden regime shift by CP-9 and bringing the system to the lowest levels of photosynthesis and growth.

Between ~600 and 200 cal. yr BP, the coarser fractions and P contents slightly increase, although sheath:belowground ratio, productivity and OM accumulation show low values. This chronological interval is coeval with the establishment of terraced fields of olive trees and vineyards in the area (Franquesa i Codinach, 1995). Terraced agriculture would have limited soil erosion and hence the fluxes of sediments and nutrients into the bay, as attested by the decrease in the abundance of foraminiferal linings (Fig. 5; López-Merino et al., 2017). This lower input of nutrients would explain the lower values of sheath:belowground ratio (Fig. 5).

Although sediment and nutrient inputs into the bay were reduced during phase III, this was not paralleled by a recovery in the productivity levels. The still low prevailing TSI may have kept productivity at its lowest levels, although the crossed threshold in the resilience of the meadow could have meant a change in the functioning of the ecosystem.

#### 5.3.4. *Phase IV: Low productivity despite better environmental conditions (~200 cal. yr BP-present)*

During the last two centuries OM accumulation decreases, ecosystem productivity shows low values with no clear trend, the coarser fractions increase, and the sheath:belowground ratio shows higher values. Agriculture practices in the area were progressively abandoned since AD ~1850 due to phylloxera plague damaging the vineyards, and since 1956 CE after a damaging frost (Franquesa i Codinach, 1995). The progressive abandonment of the terraced fields could have enhanced catchment soil erosion, being the reason behind the increase in the coarser fraction, in P content and sheath:belowground ratio.

Briefly, during this phase, even though TSI is higher, the seagrass meadow does not recover its previous state of productivity. This might be because the trespassed threshold at CP-9.

The results of pRDA for the record of ecosystem productivity composite variable (PC4) show a quite equally distributed variability between local and large-scale factors as well as their interaction (Fig. 6). Therefore, during the last four millennia the ecosystem productivity have been affected by both human impact and climate, although their importance seems to have varied for the different phases. The long-term perspective of the mechanisms that control productivity in the *P. oceanica* ecosystem provided by the application of a palaeoecological approach on the seagrass mat, are coherent with the controls for the seasonal growth in this species in shallow environments, where local factors can play a major role when light availability is high (Alcoverro et al., 1995).

## 6. Conclusions

The combination of biological and sedimentological proxies has provided long-term information on the functioning of the *P. oceanica* ecosystem. The multi-proxy analysis has revealed millennial to centennial-scale seagrass ecosystem dynamics through changes in the OM accumulation in the mat, ecosystem productivity, nutrient supply and catchment soil erosion. Global (TSI and NH temperature) and local (anthropogenically-derived nutrient and sediment inputs) factors, as well as their interactions have played a role in the dynamics of the *P. oceanica* ecosystem throughout the last four millennia.

Although the multi-proxy approach has provided unvaluable long-term information on ecosystem changes, the knowledge gaps on the relationships between the proxies used and the environmental factors they are supposed to represent should not be ignored. More integrated studies are needed in order to get a better understanding of catchment-bay interactions, since local factors in the catchment seem to be as important as the climate effects.

The results obtained here, together with the overall ecosystem trends identified, largely match with those found by López-Merino et al. (2017) for another core at the same study area (150 m apart) and using another set of proxies. This reinforces our confidence in the robustness of the approach and in the usefulness of paleaeoecology as a tool for conservation. An overarching recommendation to be drawn from this study is the need of extending the observation level at the catchment scale if we do not want to overlook key factors that can bring coastal ecosystems close to crossing critical thresholds beyond their resilience.

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# Factors regulating primary producers' assemblages in *Posidonia oceanica* (L.) Delile ecosystems over the past 1800 years

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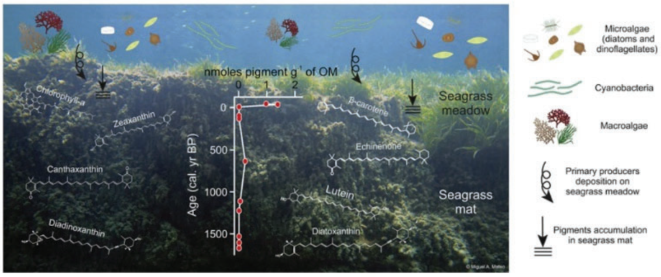
## HIGHLIGHTS

- Fossil pigments can be used to reconstruct seagrass phototrophic community.
- Phototrophic community composition was affected by local and global factors.
- Global climate factors explained long-term changes in the dinoflagellates abundance.
- Global warming may favour the development of dinoflagellates in seagrass meadows.
- Phototrophic community changes might impact the seagrass ecosystem functioning.

## GRAPHICAL ABSTRACT



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## ABSTRACT

*Posidonia oceanica* (L.) Delile meadows are highly productive coastal marine ecosystems that provide multiple ecosystem services. The seagrass is not always the major contributor to total primary production, however, little is known about long-term changes in the composition of primary producers within seagrass meadows. Understanding compositional shifts within the community of primary producers is crucial to evaluate how climate and anthropogenic change affect the functioning of seagrass ecosystems. Here we analysed marker pigment composition in seagrass cores from two bays of the Cabrera Island (Balearic Islands, Spain) to asses long-term changes in phototrophic community composition and production in seagrass meadows, and identify the environmental factors triggering those changes. The proxy dataset was explored using principal component analyses (PCA): one including the pigment dataset to look for associations between producers' groups, and another one combining the pigment dataset with plausible local and global regulatory factors to assess the environmental drivers of change. Analyses of characteristic pigments and morphological fossils (cysts) showed that the abundance of dinoflagellates increased over the last 150–300 years, coeval with a rise in solar irradiance and air temperature. When compared among embayments, pigments from cyanobacteria predominated in seagrass meadows located at Es Port, a sheltered bay receiving higher terrestrial runoff; whereas pigments from diatoms, seagrasses and

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rodophytes were more common at Santa Maria, an exposed bay with clearer waters. Water depth also played a role in controlling the phototrophic community composition, with greater abundance of diatoms in the shallowest waters (<5 m). Overall, our results suggested that historical and spatial variation in seagrass meadows' phototrophic community composition was influenced by the interaction between local factors (catchment-bay characteristics) and global climate processes (energy influx). Together these patterns forecast how marine primary producers and seagrass ecosystem structure may respond to future global warming.

## 1. Introduction

*Posidonia oceanica* seagrass meadows are one of the most valuable habitats in the Mediterranean Sea owing to their multiple ecosystem services (Spalding et al., 2003). However, this endemic species has exhibited widespread decline since the early 20th century, mainly due to local anthropogenic pressures such as coastal development, pollution, trawling, fish farming, moorings, dredging, dumping and introduced species (Boudouresque et al., 2009). Fortunately, de los Santos et al. (2019) showed that seagrass loss rates recently slowed down due to effective conservation and restoration actions, including habitat protection. Despite this promising news, relatively little is known about how *P. oceanica* meadows have varied historically in response to perturbations.

Therefore, elucidation of the long-term dynamics and environmental drivers of ecosystem change is required to evaluate the magnitude of current declines in an historical context, as well as to predict, prevent or mitigate the effects of present and future environmental changes on seagrass meadows structure and function (López-Merino et al., 2017; Leiva-Dueñas et al., 2018).

Total primary production of seagrass ecosystems does not always depend on the seagrass species as the major contributor. Other primary producers inhabiting the meadows can contribute substantially (up to 60% of total production), including epiphytes, phytoplankton, phytobenthos and macroalgae (McRoy and McMillan, 1977; Borowitzka et al., 2006; Mateo et al., 2006). The abundance and composition of primary producers' communities within seagrass meadows are regulated by complex mechanisms reflecting interactions between physico-chemical (e.g., light, temperature, water movement, nutrients) and biological factors (e.g., competition for space, grazing and predation) (Koch, 2001; Borowitzka et al., 2006) (Fig. 1). Regulation of composition at the decadal-scale appears to mainly involve competition for light and nutrients between micro- and macroalgae and the seagrass (Delgado et al., 1999; Hemminga and Duarte, 2000; Ralph et al., 2006). Elevated nutrient concentrations favour phytoplankton blooms, as well as epiphyte and macroalgae overgrowth, all leading to attenuation of irradiance and diminished transmission to the seagrass canopy (McGlathery et al., 2007; Viaroli et al., 2008) (Fig. 1).

Epiphyte composition in seagrass leaves is influenced by complex interactions between nutrients, light, temperature, water motion, salinity, and seagrass physiological and phenological characteristics, as well as the biotic interactions between epiphytes, herbivores and predators (Armitage et al., 2006; Lavery et al., 2007; Prado et al., 2007; Mabrouk et al., 2014). In addition, epiphyte assemblages often vary predictably along a depth gradient due to changes in light, local hydrodynamics, and meadow structure (Borowitzka et al., 2006; Tsirika et al., 2007; Nesti et al., 2009; Piazzi et al., 2016) (Fig. 1).

Research on the factors regulating the complex interactions influencing coastal marine ecosystem production and composition over centennial timescales lags behind that of lacustrine and terrestrial habitats, mainly because of the relative scarcity of reliable coastal marine archives owing to their hydrodynamism (Hay, 1974; Mateo et al., 2010). *P. oceanica* meadows are an exception, since coherent sequences with high temporal resolution (2–17 yr $cm^{-1}$) can be obtained in them (Serrano et al., 2012; Serrano et al., 2016a). These *Posidonia* environmental archives, known as mats, consist of large pools of organic matter accumulated over millennia, mainly as decay-resistant plant debris and organic or inorganic remains of other meadow-inhabiting organisms (Mateo et al., 1997; Lo Iacono et al., 2008; Kaal et al., 2016). Therefore, mats can potentially preserve a wide range of biotic and abiotic

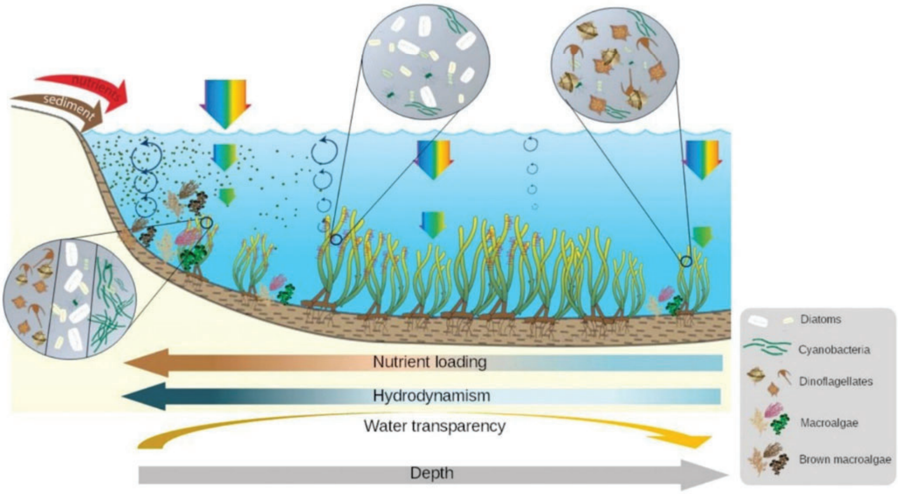

**Fig. 1.** Schematic diagram illustrating how nutrient and sediment inputs affect aquatic primary producers in seagrass meadows. Zooms are for micro-epiphytic community composition. Diagram made using image vectors from Image library in Integration and Application Network (ian.umces.edu).

proxies due to the prevailing anoxic conditions (Mateo et al., 2006; Piñeiro Juncal et al., 2018).

Proxy analyses on *Posidonia* mats allow quantification of diverse long-term environmental and ecological changes as, for example, the impact of land-use change and metal pollution on coastal systems, the role of climatic factors and seagrass revegetation in carbon burial, and historical variation in seagrass productivity (López-Sáez et al., 2009; Mateo et al., 2010; Serrano et al., 2011, 2013, 2016b, 2016c; Macreadie et al., 2015; Marba et al., 2015; López-Merino et al., 2015, 2017; Leiva-Dueñas et al., 2018). To date, however, fossils pigments from phototrophic organisms have not been used to quantify long-term changes in the production or gross community composition of seagrass systems, unlike studies on some other marine systems (Kowalewska et al., 2004; Rabalais et al., 2004; Reuss et al., 2005, 2010).

Aiming at filling the abovementioned knowledge gap, we measured past changes in concentrations of fossil pigments from diverse phototrophic organisms, in combination with other proxies (e.g., sedimentological, geochemical and dinoflagellate cysts), in five *P. oceanica* mat cores from two bays of the Cabrera National Park, Balearic Islands, Spain. The objectives of this study were: (1) to measure the variability in pigment composition through time and across spatial gradients (water depth within a bay) in two bays with contrasting features, and; (2) to identify the long-term environmental drivers which may regulate the phototrophic community composition in the meadows.

## 2. Material and methods

### 2.1. Environmental setting and coring procedures

The Cabrera Island is the largest island of the Cabrera Archipelago, located south of Mallorca (Balearic Islands) in the western Mediterranean Sea (Fig. 2). The climate of the island is semi-arid and although precipitation is scarce, there are several small watersheds that are active only during intense precipitation periods (Alcover et al., 1993). The main watershed drains into Es Port Bay (Rodríguez-Perea and Servera, 1993). The surrounding coastal waters are warm with very low nutrient content comparing to other coastal Mediterranean waters (Ballesteros and Zabala, 1993).

Five *P. oceanica* mat cores were taken in June 2015 from meadows growing in two bays: Santa Maria (SM), and Es Port (EP) (Fig. 2). Cores were collected at a single station 5-m below the sea level (bsl) at EP and along a depth-transect (5, 10, 15, and 25 m bsl) at SM (Table 1). SM is a relatively exposed bay with an area of 1.14 km$^2$ (55 m maximum depth) connected to the open sea by a 1.2-km wide mouth. On the contrary, EP (0.8 km$^2$, 45 m maximum depth) forms a relatively sheltered environment with a narrower opening (650 m) (Fig. 2). Cores were collected by scuba divers using high-density PVC pipes fitted with core catchers and a serrated leading edge. Exponential decompression functions were applied to correct for core shortening (Morton and White, 1997; Serrano et al., 2012).

At both bays, *P. oceanica* grows on biogenic, carbonate-rich and iron-deficient sediments (Holmer et al., 2005; Marbà et al., 2008). About 42%

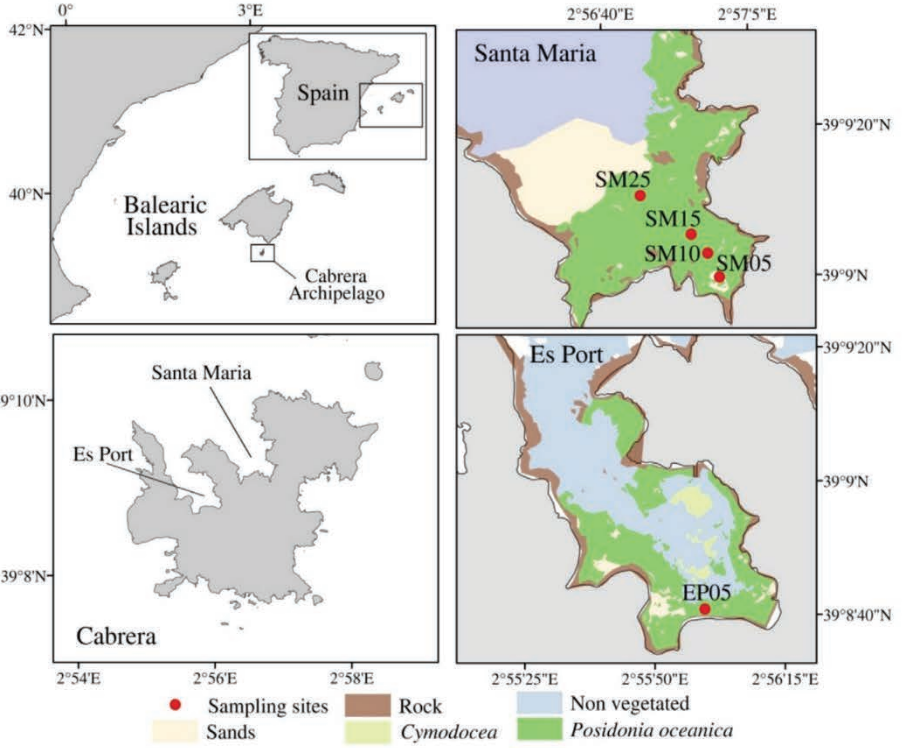

**Fig. 2.** Location of the Cabrera Archipelago as well as *P. oceanica* and *Cymodocea* meadows areal coverage in two bays: Santa Maria (SM) and Es Port (EP). Red dots indicate the core locations. The number stands for the sampling water depth (in meters below sea level).

**Table 1**
Details of the five cores taken from *Posidonia oceanica* meadows at two bays in the Cabrera Island (Balearic Islands, Spain).

| Core ID | Coordinates | | Sampling location | Water depth (m) | Compressed length (cm) | Decompressed length (cm) | Compression (%) |
|---|---|---|---|---|---|---|---|
| SM05 | 39°9′0″N | 2°56′57″E | Santa María Bay | 5 | 49 | 83 | 42.4 |
| SM10 | 39°9′3″N | 2°56′55″E | Santa María Bay | 10 | 134 | 161 | 18.3 |
| SM15 | 39°9′6″N | 2°56′53″E | Santa María Bay | 15 | 113 | 138 | 19.3 |
| SM25 | 39°9′12″N | 2°56′44″E | Santa María Bay | 25 | 84 | 89 | 5.6 |
| EP05 | 39°8′42″N | 2°55′60″E | Es Port Bay | ~5 | 88 | 98 | 17 |

of SM benthos is covered by dense, continuous *P. oceanica* meadows, whereas meadows in EP cover less area (36%) and occur at shallower depth (Marbà et al., 2002). Demographic analysis indicates that while meadows at SM are in good condition, those at EP exhibit symptoms of stress, including lower leaf production rates and vertical rhizome elongation, very low shoot recruitment, higher mortality, and elevated sulphate reduction rates. The different seagrass conditions between bays have been attributed to contrasting water residence times in EP (7–15 days) and SM (4 days) (Marbà et al., 2002; Orfila et al., 1992, 2005), and to more frequent and intensive anthropogenic activities at EP (Marbà et al., 2002).

### *2.2. Sedimentology, geochemical analyses and core chronology*

Cores were cut longitudinally and opened into two halves. One-half was analysed non-destructively for elemental composition using X-ray fluorescence (XRF) with an AVAATECH core scanner at the CORELAB laboratory, University of Barcelona. One cm-thick samples from one of the half-cores were dried at 60 °C until constant weight to determine dry bulk density, then homogenized using an automated agate mortar (Mortar Grinder RM-200 RETSCH).

Organic matter content (OM) was estimated in the samples by mass-loss-on-ignition at 550° for 4 h. Sediment grain size was determined using a laser-diffraction particle analyser (Mastersizer 2000, Malvern instruments Ltd., UK). Carbon and N elemental and isotopic composition of sediment samples were analysed at UH Hilo Analytical Laboratory, University of Hawaii at Hilo, on a Thermo-Finnegan Delta V IRMS isotope ratio mass spectrometer coupled with a Costech elemental analyser.

Isoprenoid glycerol dialkyl glycerol tetraether (GDGT) lipids were used to calculate the Branched and Isoprenoid Tetraether (BIT) index, an index of the relative abundance of terrestrial and autochthonous organic matter in marine sediments (Hopmans et al., 2004). The samples polar fraction were analysed for GDGTs according to Schouten et al. (2007). GDGT analyses were performed using liquid chromatography–mass spectrometry (LC–MS) with a Hewlett Packard1100 Series instrument equipped with an auto-injector and ChemStation chromatography manager software.

Radiocarbon ($^{14}$C) and lead-210 ($^{210}$Pb) activities were measured using accelerator mass spectrometry (DirectAMS laboratory) and alpha spectrometry (Environmental Radioactivity Laboratory, Autonomous University of Barcelona), respectively, to obtain age-depth models for the collected cores.

Raw proxy data trends are presented in Fig. S1.

### *2.3. Fossil pigment analysis*

Pigments and their derivatives were extracted, isolated, identified and quantified using high-performance liquid chromatography (HPLC) with an Agilent model 1100 instrument at University of Regina following standard methods of Leavitt and Hodgson (2001). Fossil pigment interpretations were restricted to a subset of carotenoid and chlorophyll biomarkers that commonly preserve in sedimentary deposits (Table 3). Predominant phorbins identified included metrics of total primary producers such as labile Chlorophyll-*a* (chl-*a*; a precursor), pheophytin *a* (Chl's stable product), and chlorophyte markers (chl-*b*, pheophytin *b*). Pigment preservation index (PPI) was calculated from the ratio of chl-*a* to its degradation product pheophytin *a*. Complete fossil pigment profiles are presented in Fig. S2.

### *2.4. Organic-walled dinoflagellate cysts analysis*

A palynological analysis of pollen and non-pollen palynomorphs (NPP) of the cores is currently under way. Among the NPP, we have identified organic-walled dinoflagellate cysts (dinocysts); microremains relevant for this study due to their relationship with some of the analysed pigments. The results from core EP05 and the preliminary results from core SM25 are presented herein. Pollen and NPP were isolated from seagrass deposits using standard palynological extraction protocols, including sediment digestion with HCl, NaOH and HF to eliminate carbonates, humic acids and silicates, respectively (Fægri and Iversen, 1989). Dinocysts were identified and counted using light microscopy at ×400 magnifications.

### *2.5. Numerical procedures*

Principal component analysis (PCA) was used to explore potential associations in the community of primary producers as recorded by fossil pigment concentrations in the cores ($\text{PCA}_{\text{pigments}}$). Fossil pigment data were reported in units of concentration and, as such, are compositional data which required isometric log-ratio transformation prior the analysis (Aitchison, 1986; Egozcue et al., 2003; Filzmoser et al., 2010). The analysis consisted in a robust PCA via *pcaCoDa* command in "*robcompositions*" package in the R computational environment (Templ et al., 2011).

To determine which environmental variables were the most influential on pigment marker composition, another robust PCA was run including both local factors and global climate indicators ($\text{PCA}_{\text{environmental}}$). Local factors included biotic variables such as total primary production (as chl-*a*, β-carotene and OM), nutrient cycling and organic matter supply (C and N stable isotope values and BIT index), as well as abiotic descriptors (sediment grain size, and C and N elemental composition, XRF-measured elements). Global climate external factors included indices of Total Solar Irradiance (TSI, Vieira et al., 2011), Northern Hemisphere Temperature (NHT, Kobashi et al., 2013) and the North Atlantic Oscillation (NAO; Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012) - NAO is an atmospheric mode affecting the hydrological variability in the western Mediterranean (Roberts et al., 2012).

Generalized additive models (GAMs) were used to estimate temporal trends in the principal components scores and dinocyst concentrations. GAMs are able to model non-linear relationships between time and a response variable and can handle the irregular spacing typical in palaeoecological time series (Simpson, 2018). Thin-plate regression splines were used to parametrise the smooth functions of time (Wood, 2003). The differences between the fitted smooth functions for $\text{PC1}_{\text{pigments}}$ scores and concentrations of dinocysts were calculated as in Rose et al. (2012). GAMs were performed using the mgcv package in R (Wood, 2004, 2017, Wood et al., 2016).

*All statistical* analyses were conducted using R statistical software (R Core Team, 2018) and detailed descriptions of the materials and methods section are given in Supplementary Material.

## 3. Results

### 3.1. Age-depth models

The age-depth models combining radiocarbon and $^{210}$Pb dates revealed that core SM15 extended back to ~1900 cal. yr BP, whereas cores SM25 and EP05 extended to ~1700 cal. yr BP (Table 2, Fig. 3A). Cores SM05 and SM10 encompassed less time, SM05 dated back to ~100 and SM10 to ~700 cal. yr BP. Overall, accumulation rates varied between 0.02 and 2 cm/yr with significantly differences among cores (median Kruskal-Wallis test, $p < 0.05$). A nonparametric pairwise multiple comparison (Dunn's test, $p < 0.05$) confirmed all median rates were significantly different with the exception of the pair EP05 - SM15 ($p = 0.754$). Accumulation rates decreased with increasing water depth in SM, from a median of 0.36 cm/yr (SM05) to a median of 0.06 cm/yr (SM25) (Fig. 3B). In most cores, mat accumulation was likely continuous with the exception of EP05 which exhibited an apparent hiatus between ~ 300 and ~1250 cal. yr BP - based on a large jump of ~950 calibrated years between two radiocarbon dates at 60 and 64 cm depth in the core (Fig. 3A and Table 2).

### 3.2. Primary producers' composition

Trends in the pigment composition within all cores were well described using a robust PCA with two principal axes, explaining 91% of the total variance (Fig. 4A). The first principal component ($PC1_{pigments}$, 78%) showed a high positive loading for diadinoxanthin (dinoflagellates, diatoms and chrysophytes) and moderate negative loadings for echinenone (total cyanobacteria), lutein-zeaxanthin (chlorophytes, higher plants, rhodophytes and cyanobacteria) and canthaxanthin (Nostocales –cyanobacteria–) (Fig. 4A and Table 4). The second principal component ($PC2_{pigments}$, 13%) showed high positive loadings for diatoxanthin (mainly diatoms) and lutein-zeaxanthin (chlorophytes, higher plants, cyanobacteria and rhodophytes), and high-to-moderate negative loadings for echinenone (total cyanobacteria) and canthaxanthin (Nostocales –cyanobacteria–) (Fig. 4A and Table 5).

The main temporal trend observed in all cores was an increase in $PC1_{pigments}$ scores towards the present, particularly during the last ~150–300 years. This trend mainly reflects increasing concentrations of diadinoxanthin (Fig. 4B). Sample scores from $PC2_{pigments}$ did not show a consistent change through time, although they did show an evident spatial pattern, with different pigment composition between bays (Fig. 4). Higher proportions of diatoxanthin and lutein-zeaxanthin were found in SM, while canthaxanthin and echinenone predominated in EP. Within SM, sample scores indicated a greater abundance of diatoxanthin and lutein-zeaxanthin in the shallowest area (SM05) of the bay (Fig. 4B).

### 3.3. Relationship between fossil pigment composition and environmental factors

A robust PCA explained 57% of the variance in fossil pigment composition using a combination of local and global predictive variables (Fig. 5A and Table 5). The first axis ($PC1_{environmental}$) accounted for 31% of the total variance and showed that diadinoxanthin was strongly and positively correlated with global climate indicators (TSI and NHT). Diadinoxanthin content was also moderately and positively correlated to $\delta^{13}$C, concentrations of chl-*a*, and the PPI. Echinenone and lutein-

**Table 2**
Radiocarbon dates in the *P. oceanica* mat cores retrieved at the Cabrera Island. The *marine 13* $^{14}$C calibration curve (Reimer et al., 2013) was used for calibration of the radiocarbon dates together with and a local marine reservoir effect (mean ± SD; $\Delta R = 26 \pm 24$ years; Riera Rullan, 2016).

| Core | Laboratory code | Decompressed depth (cm) | AMS $^{14}$C date (yr BP) | | | Cal. yr BP (2σ range) | | | Weighted mean age |
|---|---|---|---|---|---|---|---|---|---|
| EP05 | D-AMS 014002 | 32 | 398 | ± | 23 | 58.5 | – | 92.4 | 75.8 |
| | D-AMS 019447 | 34 | 379 | ± | 24 | 66.7 | – | 108 | 87.1 |
| | D-AMS 014003 | 43 | 467 | ± | 27 | 104 | – | 190 | 141.3 |
| | D-AMS 012768 | 54 | 502 | ± | 27 | 166 | – | 277 | 215.4 |
| | D-AMS 029626 | 60 | 545 | ± | 30 | 202 | – | 349 | 263.6 |
| | D-AMS 019448 | 64 | 1741 | ± | 28 | 1185 | – | 1531 | 1369 |
| | D-AMS 012769 | 75 | 1940 | ± | 26 | 1305 | – | 1620 | 1468.9 |
| | D-AMS 012770 | 96 | 1788 | ± | 29 | 1473 | – | 1473 | 1651.6 |
| SM05 | D-AMS 012771 | 57 | 75 | ± | 26 | 18.8 | – | 51.1 | 33.9 |
| | D-AMS 012772 | 68 | 105 | ± | 28 | 43.2 | – | 87.4 | 64.6 |
| | D-AMS 013117 | 78 | 366 | ± | 25 | 66.5 | – | 120 | 92.9 |
| | D-AMS 012773 | 79 | 439 | ± | 25 | 69.1 | – | 122 | 95.7 |
| SM10 | D-AMS 019434 | 34 | 104 | ± | 25 | −0.9 | – | 7.2 | 3.2 |
| | D-AMS 019436 | 58 | 449 | ± | 28 | 83.9 | – | 163 | 117.6 |
| | D-AMS 019437 | 63 | 384 | ± | 29 | 103 | – | 138 | 141.1 |
| | D-AMS 019438 | 70 | 479 | ± | 26 | 130 | – | 228 | 177.1 |
| | D-AMS 022098 | 88 | 593 | ± | 61 | 225 | – | 334 | 275.2 |
| | D-AMS 022099 | 110 | 740 | ± | 34 | 348 | – | 462 | 405.6 |
| | D-AMS 022100 | 124 | 970 | ± | 45 | 434 | – | 551 | 494.6 |
| | D-AMS 022102 | 152 | 1063 | ± | 43 | 588 | – | 740 | 657.5 |
| SM15 | D-AMS 019444 | 50 | 610 | ± | 24 | 89.4 | – | 242 | 151.8 |
| | D-AMS 012774 | 55 | 573 | ± | 23 | 126 | – | 305 | 207.6 |
| | UBA-32342 | 75 | 1732 | ± | 32 | 752 | – | 1154 | 996.7 |
| | D-AMS 019445 | 78 | 1508 | ± | 29 | 899 | – | 1169 | 1044.9 |
| | D-AMS 012775 | 89 | 1583 | ± | 23 | 1058 | – | 1269 | 1163.3 |
| | D-AMS 012776 | 104 | 2447 | ± | 32 | 1269 | – | 1703 | 1477.9 |
| | D-AMS 029627 | 120 | 2106 | ± | 29 | 1482 | – | 1845 | 1664.7 |
| | D-AMS 029628 | 135 | 1556 | ± | 29 | 1634 | – | 2098 | 1830.1 |
| SM25 | D-AMS 019439 | 8 | 216 | ± | 46 | −49.5 | – | 63.9 | 7.3 |
| | D-AMS 014000 | 28 | 508 | ± | 20 | 76.7 | – | 243 | 165.3 |
| | D-AMS 019440 | 35 | 608 | ± | 27 | 144 | – | 303 | 229.2 |
| | D-AMS 014001 | 39 | 604 | ± | 29 | 181 | – | 383 | 271.8 |
| | D-AMS 012777 | 49 | 1000 | ± | 27 | 427 | – | 637 | 537.7 |
| | D-AMS 019441 | 56 | 1234 | ± | 27 | 628 | – | 852 | 728 |
| | D-AMS 012778 | 70 | 1957 | ± | 24 | 1170 | – | 1525 | 1374.6 |
| | D-AMS 019442 | 76 | 1985 | ± | 25 | 1428 | – | 1533 | 1532.2 |
| | D-AMS 012779 | 89 | 2178 | ± | 28 | 1619 | – | 1871 | 1748.5 |

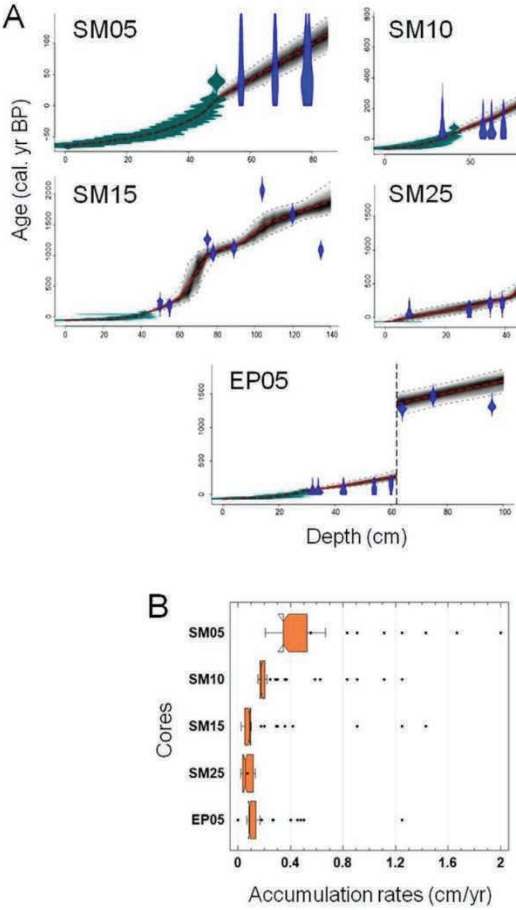

**Fig. 3.** A) Bayesian age depth-models of Cabrera Island cores using Bacon. R software (Blaauw & Christen, 2011). Lead-210 (in green) and radiocarbon (in blue) dates were included in the age-depth models. Radiocarbon dates were calibrated using the *marine 13* calibration curve (Reimer et al., 2013) and corrected for a local marine reservoir effect (mean ± SD; ΔR = 26 ± 24 years; Riera Rullan, 2016). The red dashed curve shows the "best" model based on the weighted mean age for each depth. Individual radiocarbon dates are shown in probability density functions of calibrated ages. The grey area indicates the uncertainty envelope of the model with grey dashed curves indicating 95% confidence intervals. The vertical, dashed black line on the EP05 model denotes a hiatus. B) Notched box-plot of accumulation rates for each of the sampled cores.

zeaxanthin abundances were also correlated moderately and negatively with diadinoxanthin (Fig. 5A).

$PC2_{environmental}$ accounted for 26% of the total variation (Fig. 5A). On this axis, abundances of diatoxanthin and lutein-zeaxanthin were positively correlated with chlorine, medium and fine-sands, PPI and chl-*a* content, while negatively correlated with echinenone and canthaxanthin. In contrast, echinenone and canthaxanthin were positively correlated with OM, $\delta^{15}N$, the BIT index, coarse-sandy fractions and β-

**Table 3**
Pigments identified in the *P. oceanica* mat cores in this study as well as their taxonomic affinities.

| Pigment | Algal group(s) |
|---|---|
| Alloxanthin | Cryptophytes |
| Diadinoxanthin | Dinoflagellates, diatoms, chrysophytes |
| Diatoxanthin | Diatoms, chrysophytes |
| Lutein- Zeaxanthin | Higher plants, chlorophytes, rhodophytes[a], cyanobacteria |
| Echinenone | Total cyanobacteria |
| Canthaxanthin | Nostocales cyanobacteria |
| β-carotene | Total phototrophs |

[a] In marine ecosystems, lutein-zeaxanthin also represents the Rhodophyta (Esteban et al., 2009).

**Table 4**
Factor loadings of the $PCA_{pigments}$ ran to explore potential associations in the community of primary producers as recorded by fossil pigment concentrations. Numbers in bold indicate pigments with highest factor loadings. Numbers in bold italics indicate pigments with moderate factor loadings.

| | $PC1_{pigments}$ | $PC2_{pigments}$ |
|---|---|---|
| Variance explained | 78% | 13% |
| Diadinoxanthin | **0.85** | −0.07 |
| Alloxanthin | 0.14 | −0.07 |
| Diatoxanthin | −0.18 | **0.55** |
| Lutein-zeaxanthin | ***−0.23*** | **0.49** |
| Canthaxanthin | ***−0.21*** | ***−0.29*** |
| Echinenone | ***−0.37*** | **−0.59** |

**Table 5**
Factor loadings of the $PCA_{environmental}$ ran to decipher relationships between marker pigment composition and explicative variables. Numbers in bold indicate variables with the highest factor loadings and in bold. Numbers in bold and italics indicate variables with moderate factor loadings. Explicative variables are the Branched and Isoprenoid Tetraether (BIT) index -an index of the relative abundance of terrestrial organic matter versus marine input in marine sediments (Hopmans et al., 2004)-, Total Solar Irradiance (TSI, Vieira et al., 2011), index of North Atlantic Oscillation (NAO, Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012), Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013), grain-size distribution, content of organic matter (OM), XRF-measured elements (Fe, Si, Ti, K, Ca, S, Cl and Br), carbon and nitrogen stable isotopes, chl-*a* and β-carotenes, and a pigment preservation index (chl-*a*/pheophytin *a*).

| | $PC1_{environmental}$ | $PC2_{environmental}$ |
|---|---|---|
| Variance explained | 31% | 26% |
| Diadinoxanthin | **−0.53** | −0.08 |
| Alloxanthin | −0.01 | 0.00 |
| Diatoxanthin | 0.08 | −0.10 |
| Lutein-zeaxanthin | 0.13 | −0.10 |
| Canthaxanthin | 0.11 | ***0.13*** |
| Echinenone | ***0.22*** | ***0.14*** |
| β-carotenes | ***0.16*** | ***0.19*** |
| chl-*a* | ***−0.16*** | ***−0.19*** |
| Mud | 0.00 | 0.06 |
| Fine sands | −0.02 | ***−0.17*** |
| Medium sands | −0.01 | ***−0.18*** |
| Coarse sands | 0.02 | **0.29** |
| Gravel | 0.00 | 0.00 |
| Si | −0.04 | −0.02 |
| S | −0.01 | 0.10 |
| Br | 0.00 | 0.08 |
| Cl | 0.00 | **−0.32** |
| K | 0.03 | 0.07 |
| Ca | 0.03 | 0.10 |
| Ti | 0.00 | 0.00 |
| Fe | 0.00 | 0.00 |
| TSI | **−0.35** | 0.11 |
| NAO | 0.01 | −0.06 |
| NHT | **−0.59** | 0.16 |
| BIT | 0.06 | **0.36** |
| $\delta^{13}C$ | ***−0.23*** | −0.05 |
| $\delta^{15}N$ | −0.02 | **0.37** |
| OM | ***−0.17*** | **0.43** |
| Preservation index | ***−0.18*** | **−0.21** |

carotene, and negatively with diatoxanthin and lutein-zeaxanthin (Fig. 5A and Table 5).

Overall, $PC1_{environmental}$ scores exhibited an increasing trend towards the present in most cores, in particular during the last 150–300 years (Fig. 5B). Temporal trends of $PC2_{environmental}$ scores showed no clear nor common pattern among cores through time, although they did show the same difference among embayments as described for $PC2_{pigments}$ (Fig. 5B).

### *3.4. Dinocyst records*

Dinocysts concentrations were low in sediments from both bays. They were 1–2 orders of magnitude higher in EP05 than in SM25 (Fig. 6). All dinocysts identified were of autotrophic affinity. In both bays, dinocyst concentrations were composed predominately of *Spiniferites* spp. and *Lingulodinium machaerophorum*. *L. machaerophorum* is the cyst produced by the motile form *Lingulodinium polyedrum*, a species which inhabits estuaries and coastal bays worldwide, including the Mediterranean Sea (Lewis and Hallett, 1997; Penna et al., 2006). The most notable feature of the dinocyst records is the presence of a trend towards increasing concentrations during the last two centuries, particularly for *Spiniferites* spp., *L. machaerophorum*, *Operculodinium* spp., and for total dinocysts (Fig. 6). These trends were significant only for EP05, which is perhaps related to the larger amount of samples processed in EP05 compared to SM25.

GAMs were employed to test if the temporal changes in concentrations of dinoflagellate pigment diadinoxanthin (as $PC1_{pigments}$ scores) were similar to those recorded for dinocysts (Fig. 7). Here the differences between the GAM-fitted pigments and cyst trends were estimated only for the most recent 250 yrs., the period during which there was directional change in fossil abundance in EP05. Comparisons were conducted between $PC1_{pigments}$ and total cyst concentrations (TC), as well as between $PC1_{pigments}$ and cysts from *Lingulodinium machaerophorum* (LM) and *Spiniferites* spp. (SS). Confidence intervals not encompassing zero, are indicative of significant differences between the smoothed trends (Rose et al., 2012). In EP05 core, no difference was observed between trends in any metric of cyst abundance (TC, LM or SS) and PC1 scores during the last 250 years (Fig. 7). Therefore, we infer that the increasing recent trend in $PC1_{pigment}$ and by inference the dinoflagellate biomarker diadinoxanthin mainly reflect changes in fossil concentrations of dinoflagellate cysts at least in the EP05 core (Figs. 6 and 7).

## 4. Discussion

### *4.1. Seagrass phototrophic community*

The overall composition of sedimentary pigments from the mat cores was consistent with the expected assemblage of primary producers observed in *P. oceanica* meadows. In general, modern macroalgal species are characteristically composed mainly of calcareous Rhodophyta and non-calcified Ochrophyta, whereas microalgal epiphytes usually include diatoms, dinoflagellates and cyanobacteria in declining relative abundance (Piazzi et al., 2016; Agawin et al., 2017). Similarly, the modern phytoplankton assemblages are mainly composed of diatoms and dinoflagellates (Moncer et al., 2017), while the water column near Cabrera is known to harbour a great abundance of pico and nanoplankton, dinoflagellates, coccolitophorids and diatoms (Vives, 1993). We suggest that seagrass, possibly in association with rhodophytes, is the main source of the couplet lutein-zeaxanthin, as it is the most abundant carotenoid in live *P. oceanica* tissues (Casazza and Mazella, 2002).

### *4.2. Observed temporal and spatial patterns*

Multivariate analysis of the cores revealed two main patterns of change in the fossil pigment assemblages. First, we recorded a temporal shift in the abundance of dinoflagellates and siliceous algae, which appears to reflect the influence of global climate change, particularly the inputs of energy as irradiance and heat (i.e., TSI and NHT). Second, our results showed clear spatial patterns in primary producers' community composition, seemingly related to embayment-specific local conditions (EP versus SM), and to the water depth gradient (SM gradient). Taken together, these patterns suggest that primary producers in seagrass meadows are influenced by a combination of global and local regulatory mechanisms.

#### *4.2.1. The recent increase in dinoflagellates*

Increased abundance of dinoflagellates and possibly siliceous taxa (as the carotenoid diadinoxanthin) was observed among all cores over the last 150–300 years (Figs. 4 and 5). Our results suggest that the carotenoid diadinoxanthin was more abundant during episodes of high solar irradiance (i.e., TSI), air temperature (i.e., NHT) and, to a lesser extent, ecosystem production (i.e., $\delta^{13}C$ and chl-*a*) according to $PC1_{environmental}$ (Fig. 5A). Hence, changes in dinoflagellate abundance seem to be influenced by global climate variables - specifically the input of energy as irradiance and heat. Changes in pigment preservation may also partly explain these historical trends, as noted with the direction of the pigment preservation index vector (Fig. 5A). Post-depositional degradation may contribute to the decline in labile diadinoxanthin with increasing sediment age ($PC1_{pigments}$ and $PC1_{environmental}$, Figs. 4B and 5B). However, analysis of resting cysts from dinoflagellates in cores EP05 and SM25 also showed an increase in dinoflagellate abundance over the same period, especially for *L. machaerophorum* and *Spiniferites* spp. in EP05 (Fig. 6). Dinocysts are composed of highly resistant

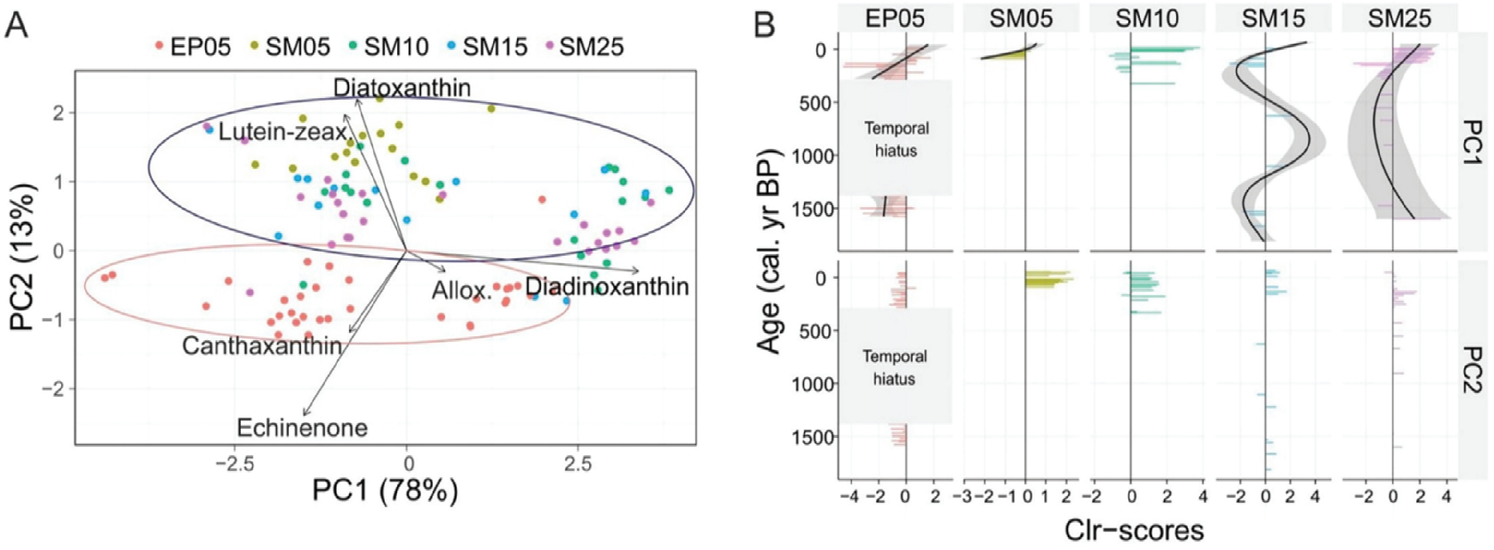

**Fig. 4.** PCA$_{\text{pigments}}$ run to explore potential associations in the community of primary producers as recorded by fossil pigment concentrations in the cores. **A)** Clr-biplot of sample scores. Red ellipse indicates samples from EP and blue ellipse indicates samples from SM. **B)** Depth records of the PC$_{\text{pigments}}$ scores. Black solid lines indicate fitted smooth functions of time (GAM models, formula = $y \sim s(x)$) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant trends are shown ($p > 0.05$). Algal groups associated to pigments are in Table 3.

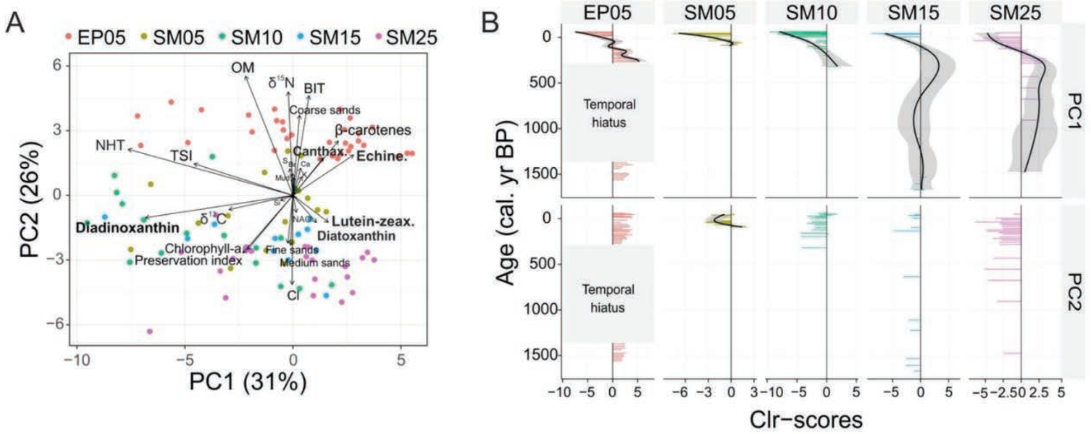

**Fig. 5.** $PCA_{environmental}$ run to decipher relationships between fossil pigment composition and explicative variables: BIT index -an index of the relative abundance of terrestrial organic matter versus marine input in marine sediments (Hopmans et al., 2004), Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012), Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013), grain-size distribution, content of organic matter (OM), XRF-measured elements (Fe, Si, Ti, K, Ca, S, Cl and Br), carbon and nitrogen stable isotopes, chl-*a* and β-carotenes, and a pigment preservation index (chl-*a*/pheophytin *a*). **A)** Clr-biplot of sample scores. **B)** Depth records of the $PC_{environmental}$ scores. Black solid lines indicate fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant trends are shown ($p > 0.05$). Algal groups associated to pigments are in Table 3.

organic compounds, which are preserved well in sediments (Versteegh and Blokker, 2004). Given the strong concordance between historical trends in the dinoflagellate biomarker diadinoxanthin (as $PC1_{pigments}$) and dinoflagellate cyst concentrations, we infer that increased abundance of diadinoxanthin over the past ~250 years reflects actual changes in algal biomass, rather

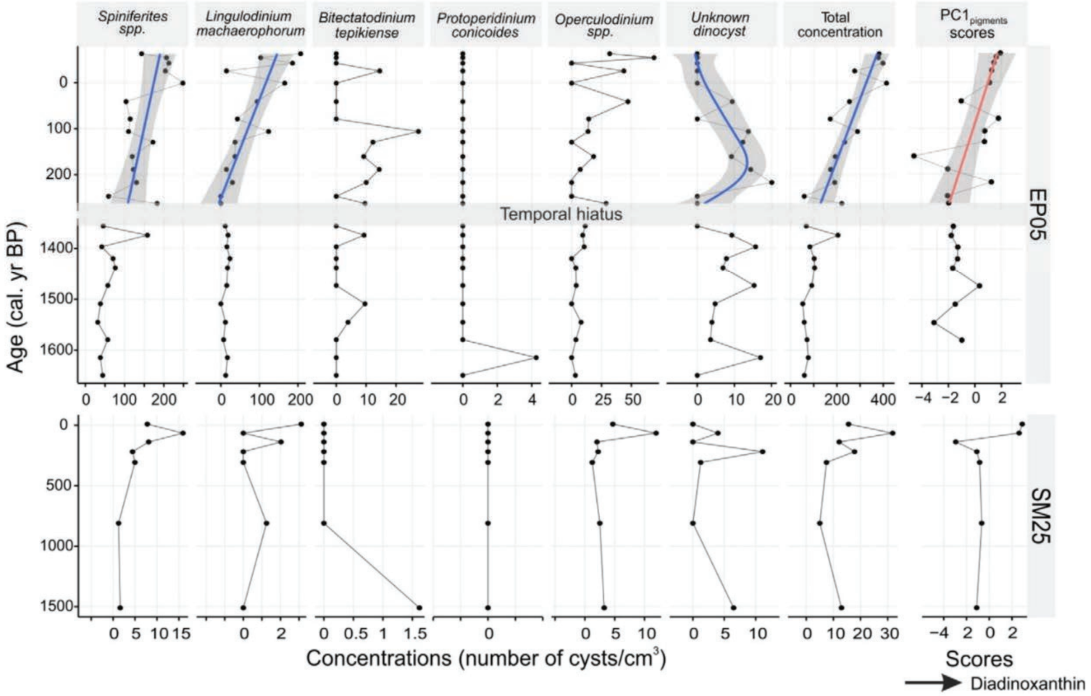

**Fig. 6.** Dinocyst concentrations records of cores EP05 and SM25 plotted together with $PC1_{pigments}$ scores. Positive scores of $PC1_{pigments}$ are related with higher concentrations of diadinoxanthin. Coloured solid lines indicate fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant trends are shown ($p > 0.05$).

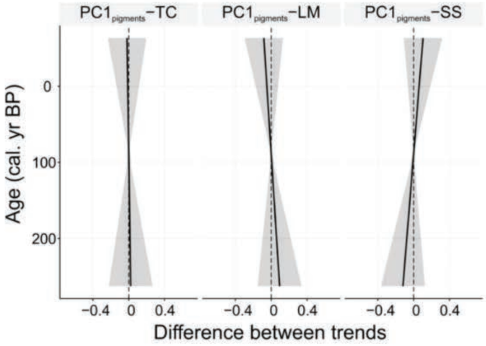

**Fig. 7.** Differences between fitted trends in the scores of $PC1_{pigments}$ and dinocysts records for the last 250 years in EP05. Black solid lines indicate differences between fitted smooth functions of time (GAM models, formula = y ~ s(x)) of $PC1_{pigments}$ scores, concentrations of total dinocysts (TC), *Lingulodinium machaerophorum* (LM) and *Spiniferites* spp. (SS). Grey shaded regions are 95% point-wise confidence intervals on these differences.

than slow post-depositional degradation in the *Posidonia* seagrass mats.

The observed orthogonal relationship between diadinoxanthin and diatoxathin in the two PCAs was unexpected because both pigments usually co-occur in several algal groups, as in diatoms and dinoflagellates. Although speculative, this lack of correlation could be due to the fact that they are associated with different algal groups in the particular setting of Cabrera: diadinoxanthin with dinoflagellates and diatoxanthin with diatoms. Regardless, the uncorrelated nature of historical trends in diadinoxanthin and the diatom-specific biomarker diatoxanthin again suggests that historical trends in diadinoxanthin were recording mainly changes in marine dinoflagellate abundance.

Increased abundance of dinoflagellates during periods of elevated solar irradiance may be related to their ability to produce substantial amounts of UV-absorbing photo-protective compounds under high irradiance (Hannach and Sigleo, 1998). In this sense, diadinoxanthin is known to act as a photoprotective accessory pigment (Lavaud et al., 2002; Laviale and Jacques, 2011). Diadinoxanthin is not only present in dinoflagellates but also in some species of raphidophytes (e.g., *Heterosigma akashiwo, Chattonella subsalsa*), which also thrive in high UV environments (Fu et al., 2012; Wells et al., 2015). Similarly, elevated water temperature may favour growth of epiphytic dinoflagellates and diatoms in seagrass meadows (Johnson et al., 2005; Turki, 2005; Frankovich et al., 2006; Mabrouk et al., 2012). Moreover, the correlation between dinoflagellates and temperature found here was also described in several long-term dinocyst records, in which high *L. machaerophorum* and *Spiniferites* spp. abundance correlated with warmer sea surface waters and stronger stratified conditions in coastal areas (Pospelova et al., 2006; Sobrino et al., 2012; Bringué et al., 2013; Leroy et al., 2013). Those studies also reported sharp increases in *L. machaerophorum* over the last century, similar to the patterns observed in this study (Fig. 5A). *L. machaerophorum* is also a potentially-toxic taxon, known to produce yessotoxins (e.g. Paz et al., 2004; Armstrong and Kudela, 2006). Therefore, their higher abundance could increase the risk of toxic algal blooms that could affect the entire ecosystem composition and structure (Sellner et al., 2003).

Our results provide a predictive understanding of the response of phototrophic assemblages in seagrass meadows to global change. Specifically, we anticipate an increase in dinoflagellates as a consequence of global warming. The exact consequences of this change in the composition of primary producers are so far unknown. Our study points to a greater contribution of autotrophic dinoflagellates to autotrophic production in seagrass meadows, possibly leading to the outcompetition of the seagrass (Fig. 5A). Providing dinoflagellates do not outcompete the seagrass and go through mass encystment, they could even have an effective contribution to carbon sequestration (Spilling et al., 2014; Wasmund et al., 2017). However, the latter speculation may be difficult to evaluate, as *P. oceanica* is thought to be negatively impacted by the on-going sea water warming (Marbà and Duarte, 2010; Savva et al., 2018).

### 4.2.2. Spatial differences between bays and along water depth

Our results revealed pronounced spatial patterns in primary producer community composition, caused by site-specific local effects, as well as the natural depth gradient. In the anthropogenically-impacted EP setting, the community was mainly dominated by cyanobacteria (as canthaxanthin and echinenone), whereas diatoms (as diatoxanthin), chlorophytes, rhodophytes and, most probably, the seagrass (all as lutein-zeaxanthin) were more characteristic of the less disturbed SM setting. As detailed below, these patterns may arise because of basin-specific differences in local land use and catchment characteristics, specifically nutrient and terrestrial organic matter inputs.

The cyanobacteria-rich community of EP developed in an environment with elevated organic matter and nutrient inputs, mainly of terrestrial origin (high loadings for BIT index, $\delta^{15}N$ and OM in $PC2_{environmental}$, Fig. 5). In EP, higher microbial decay would also explain the $\delta^{15}N$ enriched sediment organic matter relative to that of SM (Craine et al., 2015). Aside from high nutrient availability, EP waters have other physical conditions favourable to elevated cyanobacterial abundance compared to SM, such as longer water residence times and enhanced stratification (Orfila et al., 2005; Paerl and Huisman, 2008). On the other hand, diatoms, the seagrass and likely, rodophytes prevailed in SM (Fig. 4A), where organic matter is mainly derived from marine autochthonous production, as indicated by a high loading for chlorine in $PC2_{environmental}$ (Fig. 5A), an element known to be incorporated in labile marine organic matter (Leri et al., 2015). Our findings support those of Holmer et al. (2003, 2004) who reported an organic enrichment and higher mineralization rates in EP, as well as a significantly higher net community production in SM, reflecting higher light availability, lower terrestrial inputs and higher water turnover rates.

Studies of phytoplankton communities in marine waters have observed increases in the abundance of cyanobacteria under ammonium enrichment, whereas diatoms more commonly bloom when exposed to elevated nitrate concentrations (Berg et al., 2003; Heil et al., 2007; Glibert et al., 2014). Cyanobacteria are generally considered specialists that have a superior ammonium uptake kinetics (Blomqvist et al., 1994; Lindell and Post, 2001). Further, cyanobacteria can use organic matter as a nitrogen source in both lakes and marine ecosystems (e.g., Berman, 2001; Sakamoto & Bryant, 2001; Berg et al., 2003; Glibert et al., 2004; Donald et al., 2011). Therefore, the predominance of cyanobacteria in EP could reflect an elevated influx of ammonium or other N species as a result of the enhanced organic matter decomposition in this bay (Holmer et al., 2004; Pérez et al., 2007), or higher availability of dissolved organic matter. The naturally high organic matter accumulation in EP arises from discharges of the main pluvial network of the island (Rodríguez-Perea and Servera, 1993), and from the longer water residence time in EP, which, together, may favour particle sedimentation and a larger contribution of allochthonous organic matter to the bottom deposits. In fact, Mazarrasa et al. (2017) observed that allochthonous carbon accounted for more carbon in meadows from EP than in other Balearic meadows, including SM.

At SM shallowest station (SM05, Fig. 4A), pigment assemblages indicated dominance of diatoms (diatoxanthin), seagrasses, and rhodophytes (lutein-zeaxanthin) compared to the deeper stations. A greater abundance of diatoms in the shallowest areas could be related to the diatoms' feature of developing better in turbulent, well-mixed waters (Mabrouk et al., 2011). The greater abundance of seagrass at shallower depths could be explained by higher light availability and, therefore, higher photosynthetic rates and production (Alcoverro et al., 2001). In general, water depth is a key regulator of epiphytes assemblages of seagrasses due to differences in the seagrass and meadow structural characteristics, light penetration, and hydrodynamics (Piazzi et al., 2016 and references therein).

## 5. Conclusions

The use of fossil pigments is feasible in sheltered vegetative coastal habitats. In this sense, this study pioneers in the use of fossil pigments in *P. oceanica* mats as proxy of phototrophs composition. Fossil pigments can be used in *Posidonia* spp. meadows, where chronologically ordered sequences are highly preserved in the sediments below them (i.e. the mats), but it could be also used in other smaller seagrass located in sheltered areas where sedimentation is not altered.

Our results report changes in phototrophic community composition and production in *P. oceanica* meadows at centennial scales. Analyses suggest that these changes were modulated by both local terrestrial influences and global climate factors. In particular, elevated solar irradiance and air temperature seem to have driven increases in dinoflagellates abundance over the last 150–300 years. Local environmental conditions were most likely responsible for differences in phototrophic communities between basins; apparently due to differences in terrestrial organic matter and nutrient inputs. Depth also influenced the phototrophic community composition, with greater predominance of pigments from diatoms, seagrasses and rodophytes in shallower waters.

These patterns confirm that primary producers in seagrass meadows are under complex hierarchical control by local and global regulatory mechanisms and provide better insights into potential phototrophic responses to global change. Specifically, we infer that global warming may favour the development of autotrophic dinoflagellate assemblages, which could negatively affect the ecosystem functioning by shading and outcompeting the seagrass. Future research could focus on the potential effects of these structural community changes on seagrass ecosystem functioning under predicted climate change scenarios.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.137163.

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# Long-term dynamics of production in western Mediterranean seagrass meadows: Trade-offs and legacies of past disturbances

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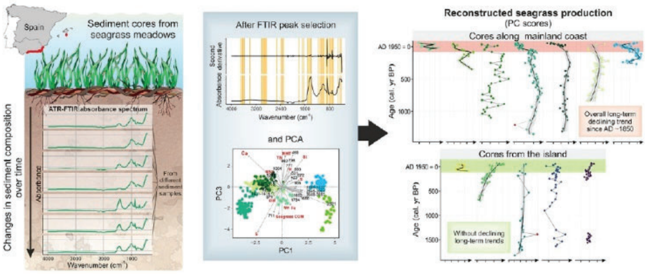
## HIGHLIGHTS

- Long-term dynamics are studied in seagrass meadows of southeastern Spain.
- This study pioneers in the use of FTIR spectroscopy in seagrass paleoreconstructions.
- Productivity decreased since AD ~1850 along the mainland coast but not in the island.
- Synergy of local and global drivers may explain the worse state of some meadows.
- Paleoecology can help identify meadows where local management can be more efficient.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Seagrasses are marine angiosperms that can form highly productive, and valuable underwater meadows, which are currently in regression. A reliable assessment of their status and future evolution requires studies encompassing long-term temporal scales. With the aim of understanding seagrass ecosystem dynamics over the last centuries and millennia, twelve sediment cores were studied from seagrass meadows located along the Andalusian coast and at the Cabrera Island (western Mediterranean). This study is pioneer in using Fourier Transform Infrared (FTIR) spectroscopy as a tool to study environmental change in seagrass sediments. FTIR is a form of vibrational spectroscopy that provides information about the sediment chemical composition. Principal Component Analysis (PCA) was used to summarise spatio-temporal data of the FTIR vibratory peaks in combination with climate and geochemical proxy data. Several PCA signals were identified: (1) one likely related to the relative changes of the main primary producers and the sedimentary environment (carbonate or siliciclastic sediments, with aromatic or aliphatic organic matter); (2) the marine community production (polysaccharides, total organic matter content and biogenic silica); and (3) the seagrass production (aromatics, carbohydrates, phenols, proteins and lipids). A decrease of seagrass production along the mainland coast was evident since AD ~1850, which may be due to combined negative impacts of seawater warming, local anthropogenic impacts, and extreme setting conditions. The legacy of these combined stressors might have influenced the current poor state of seagrass meadows in the Alboran Sea. Our results also revealed a significant

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long-term trade-off between the level of seagrass production and its temporal stability (calculated as the inverse of the coefficient of variation). This study provides a reliable baseline data, helping to assess the magnitude of seagrass regression and its drivers. This paleoecological information can help design more targeted management plans and identify meadows where local management could be more efficient.

## 1. Introduction

There is growing concern over the constant loss of coastal ecosystems, because they are among the most productive ones with fundamental processes and functions that provide a wide range of benefits to our societies (Alongi, 2002; Hoegh-Guldberg et al., 2008; Waycott et al., 2009). With the pressure of more than one-third of the world's population inhabiting coastal areas, these habitats are showing regressive trends worldwide as a consequence of local anthropogenic disturbances but also of global climate change (Millennium Ecosystem Assessment, 2005; Lotze et al., 2006; Baker et al., 2008; Davidson, 2014).

Seagrasses are marine plants that form extensive underwater meadows, one of these highly productive and threatened coastal ecosystems experiencing global loss during the 20th century (e.g. Duarte, 2002; Orth et al., 2006; Waycott et al., 2009). Their regression, although spatially variable (Waycott et al., 2009; Telesca et al., 2015), is especially worrying in the Mediterranean Sea, where seagrass meadows are the most relevant coastal habitats considering their abundance and ecological value (Ruiz Fernandez et al., 2009; Telesca et al., 2015). The main seagrass species distributed along the Mediterranean Sea are *Cymodocea nodosa* (Ucria) Ascherson, and the most abundant and endemic species *Posidonia oceanica* (L.) Delile. Since the second half of the 20th century, a declining trend has been observed for the areal extent, cover and shoot density of *P. oceanica* (Marbà et al., 2014). The regression was found not only in areas under intense anthropogenic pressure but also in relatively pristine environments (Marbà et al., 2005; Marbà and Duarte, 2010). The main drivers behind *P. oceanica* loss are considered to be water quality degradation, mechanical damage, coastal modification and extreme events that could be related to global climate change, in order of importance (de los Santos et al., 2019).

However, the evaluation of seagrass trends and the plausible causes of change are based on the observational record that began in AD ~1870 (e.g. Boudouresque et al., 2009; Marbà et al., 2014; de los Santos et al., 2019), and does not allow for a proper assessment of the role and magnitude of the present climate forcing. Paleoenvironmental reconstructions can provide a baseline of the ecosystem status previous to the onset of recent anthropogenic activities (i.e. industrial era), indicating as well how the ecosystem responded to past natural changes. Long-term information on ecosystem dynamics can greatly increase the success of conservation and management plans by providing a framework within which we can evaluate present and plausible future trends (Oldfield and Dearing, 2003).

Paleoecological studies are of special interest in *P. oceanica* meadows. This species is the largest but also one of the slowest growing with a very slow recovery as well, therefore substantial changes and responses manifest over long time scales of decades to centuries (Duarte et al., 2006; Kilminster et al., 2015). Fortunately, these ecosystems form environmental archives below the meadows, which can persist for thousands of years and enable a paleoecological approach (Mateo et al., 1997, 2002; Serrano et al., 2016a; López-Merino et al., 2017; Lafratta et al., 2018). To date, most of the seagrass paleoreconstructions have been limited to the local scale, using only one or few sediment records for the local area of interest. However, a multi-core paleoecological approach, with well-dated sediment records from several sites distributed along a region can provide a deeper and more reliable understanding of long-term processes, dynamics and drivers of change at a larger spatial scale (e.g. Reavie and Baratono, 2007; Wiklund et al., 2017). This is especially crucial in seagrass ecosystems to comprehend the spatial differences in their decline along the western Mediterranean coast (Marbà et al., 2005, 2014).

*Posidonia oceanica* forms environmental archives, also known as mats, mainly composed of organic material from all the organisms that inhabit the meadow and the overlying water column, but especially from the decay-resistant seagrass tissues, all trapped and accumulated over millennia (e.g., Kaal et al., 2016; Mazarrasa et al., 2017a). The organic material is integrated in an inorganic matrix, which can have a biogenic (in situ biologically precipitated carbonates) or lithogenic origin (erosion of coastal catchment soils) (Mateu-Vicens et al., 2012; Gaglianone et al., 2017).

The field of paleoecology in seagrass ecosystems has been gradually increasing and studies have based their results on a wide range of biotic and abiotic proxies. Some of the studied proxies are quite specific such as pollen (López-Sáez et al., 2009; López-Merino et al., 2015, 2017) or metal content of seagrass debris and sediment (Serrano et al., 2011, 2013, 2016a). However, other proxies used in seagrass paleoreconstructions are more common, like sediment organic carbon and nitrogen elemental and isotopic composition, carbonates content and grain-size distribution (Macreadie et al., 2015; Marbà et al., 2015; Serrano et al., 2016b; Mazarrasa et al., 2017a, 2017b; Leiva-Dueñas et al., 2018). However, to date, techniques providing information about more specific sediment organic and inorganic composition have not yet been used in seagrass paleoreconstructions. Infrared spectroscopy (IR) is a non-destructive analytical method that can be used for a qualitative and, when properly calibrated, quantitative identification of major changes in multiple organic and inorganic compounds across sediment layers. This technique is based on the stimulation of molecular vibrations by infrared radiation, molecular vibrations that depend on the structural, chemical bonds of the compounds. The large amount of information on inorganic and organic substances provided from each sample in a single measurement, the fact that is a fast and low-cost technique, with simple sample pre-treatments, and requiring very small amounts of sample material (<1 g) makes of this technique a tool of great potential in multi-proxy paleoecological studies (e.g. Chang et al., 2005; Vogel et al., 2008; Rosén et al., 2009, 2010; Meyer-Jacob et al., 2014; Van de Broek and Govers, 2019), as well as for assessing the ecosystems health status (Artz et al., 2008). It has even been recently applied to quantitatively determine charcoal and microplastic content in bulk sediment samples (Cadd et al., 2019; Hahn et al., 2019). However, the potential of IR spectroscopy to reconstruct paleoecological processes through relative changes in seagrass sediment compounds has yet to be explored. By elucidating the associations between the characteristic wavenumbers of Fourier transform infrared (FTIR) spectra and the compounds in seagrass sediments, our study can also set the basic knowledge needed for future investigations aiming to use FTIR for accurate quantitative estimation of main seagrass sediment components such as organic and inorganic carbon, biogenic silica, and mineralogical composition (e.g. quartz and feldspars).

Considering the potential information that can be obtained using FTIR in coastal sediments, in this study, we aim at reconstructing long-term processes and dynamics of seagrass meadows along the Mediterranean Spanish coast using a multi-core and multi-proxy approach with FTIR spectroscopy and other sedimentological proxies. The specific objectives are: (1) to evaluate the potential of FTIR spectroscopy for identifying the main organic and inorganic components in seagrass mats, in order to reconstruct the main ecological processes associated with seagrass meadows functioning; (2) to determine the variability of these processes over time and across spatial gradients, and; (3) to identify the long-term environmental drivers which may regulate the main ecological processes in the meadows studied.

## 2. Materials and methods

### 2.1. Environmental setting and coring procedures

Seagrass meadows were sampled in the western Mediterranean, along the Andalusian coast (south continental Spain), and in two bays of the Cabrera Island, the largest island of the Cabrera Archipelago (south of Balearic Islands) (Fig. 1). All cores come from *P. oceanica* meadows, except core BA, which was collected from a *C. nodosa* meadow (core BA, Table 1). Seagrass meadows in Cabrera grow on biogenic, carbonate-rich, and iron-deficient sediments, while in Andalusia, they grow on more terrigenous sediments (Marbà et al., 2005).

The climate along the Andalusian coast is subdesertic Mediterranean in the easternmost area, where the study sites RO, BA, AG, DE, and TE were located (mean annual temperature of 17.6 °C) and subtropical in the western area, where the study sites CA and ME are found (mean annual temperature of 17.2 °C; 1961–2000; CAGPDS, 2014). Precipitation in the western Andalusian area is more abundant (719 mm) and uniform than in the eastern area (236 mm; Liquete et al., 2005; CAGPDS, 2014). The climate in the Cabrera archipelago is semi-arid with a mean annual temperature of 14.6 °C and precipitation of 375 mm during the period 1950–1971 (Alcover et al., 1993). Terrestrial sediment supplies to coastal areas take place mainly under heavy episodic rainfalls. Liquete et al. (2005) proved that Andalusian river systems are quite efficient in terms of sediment delivery despite the small size of their catchments.

The Alboran Sea (where CA, ME, RO, and BA are located) is an area that shows a very high primary productivity, with cold waters, and elevated concentrations of Chl *a* mainly due to upwelling events. The high productivity in the Alboran sea is due to upwelling of nutrient-rich deeper waters. These upwellings can be wind-induced but also happen along the edges of the anticyclonic gyres of the Alboran Sea (Garcia-Gorriz and Carr, 2001). In contrast, the eastern side (where AG, DE, and TE are located) has warmer waters with lower Chl *a* content (Ramírez et al., 2005; Muñoz et al., 2015). Due to the increasing water nutrient content, turbidity is also higher towards the west. As a consequence, seagrasses grow at shallower depths and form patchier meadows the more to the west along the Andalusian coast (CAGPDS, 2018). Coastal waters surrounding the Cabrera archipelago have a very low nutrient content compared to other coastal Mediterranean waters (Ballesteros and Zabala, 1993). In fact, a trophic gradient is observed from the southwest to the northeast in the Spanish Mediterranean waters, with decreasing nutrient and chlorophyll concentrations northeastward (del Carmen García-Martínez et al., 2019). Seagrass meadows along the Iberian coast compared to those in Cabrera Island showed a higher reliance on local sources of dissolved inorganic nitrogen pools (Papadimitriou et al., 2005), while meadows located in Cabrera Island seemed to depend more on atmospheric nitrogen (Garcias-Bonet et al., 2016).

Population density and human impacts are and have been greater along the Andalusian coast compared to the Cabrera island. Denser populated areas are located in the western side of Andalusia, although some considerable urban areas also exist in the eastern side, near our study sites DE and TE. Artisanal fisheries and nautical sports activities are the main impacts in Andalusia. ME is located in a meadow where impacts from illegal wastewater discharges, trawling and *small*-scale fisheries have been observed. The study sites RO and DE are currently the most impacted meadows. RO is under multiple human pressures, such as urban wastewaters, massive tourism, mooring, trawling, and dredging. The meadow of DE has been subjected to chemical wastewater discharges since the late 1960s, and is profoundly impacted,

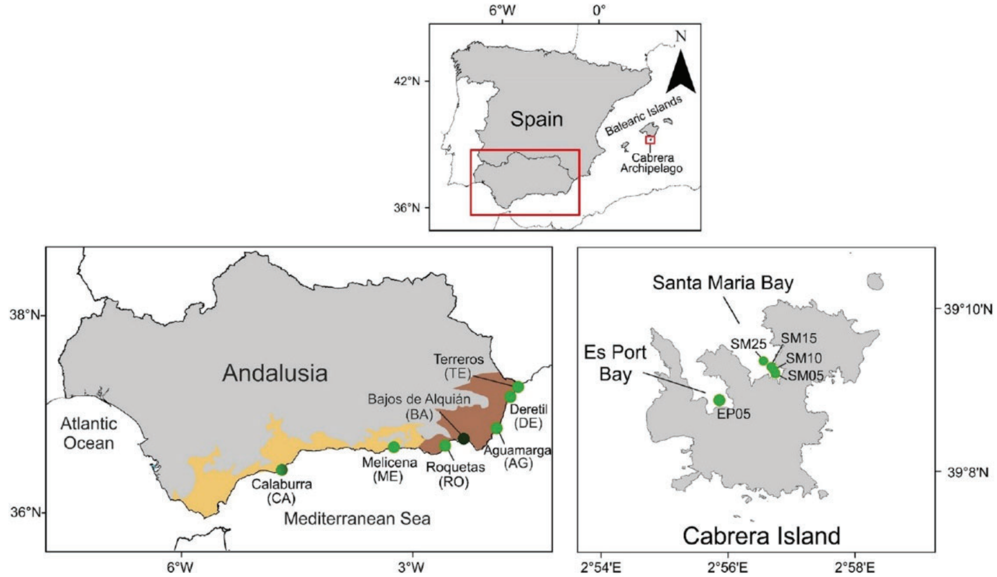

**Fig. 1.** Location of the seagrass sediment cores. Circles indicate sampling sites. Light green-coloured: *P. oceanica* meadows; dark green: *C. nodosa* meadows. The numbers in Santa Maria Bay stand for the sampling depth (in meters). In Andalusia we can see the two bioclimatic regions affecting our sampling sites, they are coloured in light orange (subtropical Mediterranean) and light brown (subdesertic Mediterranean). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Sampling sites details. Comp. (%) stands for the mean degree of compression of each core, calculated as specified in the Supplementary material.

| Region/province | Location | Coordinates | | Water depth (m) | Seagrass species | Code | Core length (cm) | Comp. (%) |
|---|---|---|---|---|---|---|---|---|
| Alboran, Málaga | Calaburras | 36°29′25.9″N | 4°41′37.25″W | 0.5 | *P. oceanica* | CA | 103 | 12.6 |
| Alboran, Granada | Melicena | 36°44′53.99″N | 3°14′3.78″W | 4.2 | *P. oceanica* | ME | 78 | 22.3 |
| Alboran, Almeria | Roquetas | 36°47′15.50″N | 2°35′20.10″W | 1.5 | *P. oceanica* | RO | 140 | 41.6 |
| Mediterranean, Almería | El Alquian | 36°49′39.1″N | 2°23′14″W | 6.8 | *C. nodosa* | BA | 117 | 9.8 |
| Mediterranean, Almería | Aguamarga | 36°56′15.66″N | 1°56′0.42″W | 4.8 | *P. oceanica* | AG | 173 | 13.1 |
| Mediterranean, Almería | Villaricos | 37°15′18.93″N | 1°45′29.53″W | 16 | *P. oceanica* | DE | 157 | 16 |
| Mediterranean, Almería | Terreros | 37°21′0.12″N | 1°40′36.37″W | 5.5 | *P. oceanica* | TE | 88 | 14.3 |
| Mediterranean, Cabrera Archipelago | Santa Maria Bay | 39°9′0″N | 2°56′57″E | 5 | *P. oceanica* | SM05 | 83 | 42 |
| Mediterranean, Cabrera Archipelago | Santa Maria Bay | 39°9′3″N | 2°56′55″E | 10 | *P. oceanica* | SM10 | 161 | 18 |
| Mediterranean, Cabrera Archipelago | Santa Maria Bay | 39°9′6″N | 2°56′53″E | 15 | *P. oceanica* | SM15 | 138 | 19 |
| Mediterranean, Cabrera Archipelago | Santa Maria Bay | 39°9′12″N | 2°56′44″E | 25 | *P. oceanica* | SM25 | 89 | 5.6 |
| Mediterranean, Cabrera Archipelago | Es Port Bay | 39°8′42″N | 2°55′60″E | 5 | *P. oceanica* | EP | 98 | 17 |

having lost the seagrass cover between its upper limit and a depth of 10–12 m (Moreno et al., 1999, 2001). The impact has been observed despite a wastewater treatment plant installed in 1999 (CMAOT, 2014). The Cabrera Island became part of a Spanish National Marine Park in 1991. There has never been a high permanent population in the island (<50 people; Frontera et al., 1993). The overall environmental conditions of the meadows in the Cabrera island are more pristine. This is especially the case in SM Bay, currently closed to visitors and with a healthy, dense, and continuous meadow until 37 m depth. However, the meadow at EP Bay is less productive and shows higher mortality rates (Marbà et al., 2002; Holmer et al., 2003). This bay receives hundreds of visitors each summer, also allowing the access to ~50 ships a day, which discharge their raw wastewaters into the bay waters (Marbà et al., 2002). The historical population of the island has been settled around EP Bay (e.g. Orfila et al., 1992), because the few arable lands were nearby (Riera Rullan, 2016). Moreover, this bay has been used as a natural harbour, providing important refuge from winds and storms (Dawson, 2013). Therefore, anthropogenic impacts in the island are and have been mainly concentrated in EP Bay.

Sediment coring was conducted in June 2015 in the Cabrera Island and in October 2016 and July 2017 along the Andalusian coast. Most cores were collected at depths ranging between 0.5 and 10 m except for a transect at 5, 10, 15, and 25 m depth in Santa Maria Bay (SM, Cabrera) (Table 1). One core was retrieved per location of study except for SM Bay, where four cores were obtained along the previous water-depth transect. Cores were collected by SCUBA divers, who manually, gently hammered and rotated high-density PVC tubes (1 and 1.5 m long and 7 cm internal diameter) into the soil. These tubes had core catchers fitted at the bottom to avoid the loss of sediment during retrieval and a serrated leading edge to favour the penetration. The empty space at the top of the core was filled with Styrofoam and then capped with a plastic tap. A bottom cap was also placed after pulling the core out of the sediment. Divers kept the core tubes vertical at all times. An exponential decompression function was applied to correct for core shortening (Morton and White, 1997; Serrano et al., 2012).

### 2.2. Laboratory analyses

Cores were cut longitudinally and opened into two halves. One-half of each core was analysed non-destructively for elemental composition using a model Avaatech XRF core scanner at CORELAB laboratory (University of Barcelona). Most of the cores were cut into 1 cm-thick samples except CA and ME (Table 1), which were cut into 2 cm-thick slices. Alternate samples were dried at 60 °C until constant weight to determine dry bulk density. Before grinding, organic seagrass debris larger than 2 mm (after sieving) were picked and weighted to obtain the coarse seagrass organic matter content (seagrass COM), and then returned to its sample, which was then homogenised using an agate mortar (Mortar Grinder RM-200 RETSCH).

The organic matter content was estimated by mass-loss-on-ignition at 450 °C for 5 h. Carbon and N elemental and isotopic composition of sediment samples were analysed on a Thermo-Finnegan Delta *V* IRMS isotope ratio mass spectrometer coupled with a Costech elemental analyser at UH Hilo Analytical Laboratory (University of Hawaii at Hilo).

FTIR spectra of the ground sediment samples were obtained using an FTIR-ATR spectrometer (Agilent Cary 630) equipped with a single-reflection diamond crystal at EcoPast laboratory (University of Santiago de Compostela). Measurements were recorded in absorption mode within the range of 4000 to 400 $\mathrm{cm}^{-1}$ at a spectral resolution of 2 $\mathrm{cm}^{-1}$ and accumulating 100 scans per sample. The background was obtained before analyzing each sample. Spectra were normalised by z-scores.

### 2.3. Sediment chronology

Samples of *P. oceanica* sheaths or *C. nodosa* debris were selected at 2–9 depths in each core for radiocarbon dating using $^{14}$C accelerator mass spectrometry (DirectAMS laboratory; Table S1) following standard procedures (Karlén et al., 1968; Stuiver and Pollack, 1977). Samples were previously rinsed as in Belshe et al. (2019). The uppermost 30 cm of each core were dated by quantification of $^{210}$Pb activities, through its daughter product $^{210}$Po, using alpha spectrometry with a PIPS detector (CANBERRA, Mod. PD-450.18 AM) at the Laboratori de Radioactivitat Ambiental (Universitat Autònoma de Barcelona). Supported $^{210}$Pb was estimated as the average $^{210}$Pb concentration of the deeper sediment layers analysed wherein $^{210}$Pb activities reached constant values. Radiometric dates were calculated using the Constant Rate of Supply (CRS) dating model (Appleby and Oldfield, 1978). Both dating methods were combined to obtain age-depth models for the collected cores. The age-depth models were developed using the Bayesian modelling approach *Bacon* (Blaauw and Christen, 2011), run in the R statistical environment (version 3.6.0; R Core Team, 2019; Fig. S1). Radiocarbon dates were expressed as calibrated years before present (cal. yr BP). Dates were calibrated using the *marine 13* $^{14}$C calibration curve (Reimer et al., 2013) and local corrections for the marine reservoir effect for the Andalusian coast ($\Delta R = 2 \pm 26$ years, Siani et al., 2000) and for Cabrera Island ($\Delta R = 24 \pm 26$ years, Riera Rullan, 2016).

### 2.4. Numerical procedures

Given the complex nature of the seagrass sediment matrix, the direct interpretation of FTIR spectroscopy is complicated because the spectral absorbance signatures are the result of many overlapped organic and inorganic compounds spectra (such as silicates, carbonates, cellulose, lignin, lipids, proteins…). To overcome this issue, the second derivative of the standardised absorbance sum spectrum was first calculated and used for wavenumber peak selection using the "andurinha" package (Álvarez Fernández and Martínez Cortizas, 2020). The strongest and most common diagnostic wavenumber peaks were selected and then analysed by principal component analyses (PCA), to explore the associations between them. The PCA enabled the correspondence between absorption peaks and specific compounds based on the fact that peaks with similar variability identified in the PCA are potentially indicative of a common precursor (Traoré et al., 2016, 2018). The assignment of correlated absorption peaks to specific inorganic and organic molecular structures was based on available literature (Table S2).

To facilitate the interpretation of the processes behind the principal components and assess their relationships with environmental drivers, local environmental and global climate variables were used together with FTIR absorption peaks in the PCA. Specifically, we included abiotic descriptors (XRF-measured elements such as Si, S, Br, Ca, Fe, Ti, Cl, K, Mn) as well as biotic variables related to total primary production (organic matter content, OM), seagrass production (seagrass COM), nutrient cycling and organic matter supply ($\delta^{13}C$ and $\delta^{15}N$). Global climate external factors included indices of Total Solar Irradiance (TSI, Vieira et al., 2011), Northern Hemisphere Temperature (NHT, Kobashi et al., 2013) and the North Atlantic Oscillation (NAO; Hurrell, 2003; Trouet et al., 2009; Olsen et al., 2012).

PCA analyses were calculated using the *pcaCoDa* command in the "robcompositions" package (Templ et al., 2011). This command allowed accounting for the compositional character of the log-ratios of XRF-elements intensities (Weltje and Tjallingii, 2008).

Generalised additive models (GAMs) were used to estimate temporal trends in the principal components scores. GAMs can model non-linear relationships between time and a response variable and can handle the irregular spacing typical in paleoecological time series (Simpson, 2018). Thin-plate regression splines were used to parametrise the smoothed functions of time (Wood, 2003). The automatic restricted maximum likelihood smoothness selection was used to select the optimal smoothness parameters (REML; Wood et al., 2016). We also checked for residual autocorrelation, and significant residual auto-correlation was not present for any of the time series.

The temporal stability of the principal components obtained was calculated using a common measure of stability, defined as the ratio of the mean ($\mu$) of the principal components scores to their standard deviation ($\sigma$) (Lehman and Tilman, 2000). The larger the value, the higher the temporal stability. To test for relationships between the temporal stability of the reconstructed ecological processes (i.e. identified principal components) and the mean level of that process (mean score value of the principal component), linear regressions were calculated. The strength of the relationship was assessed using the coefficient of determination ($R^2$). We considered the regression significant if the slope was significantly different from zero ($p < 0.05$).

All statistical analyses were conducted using R statistical software version 3.6.0 (R Core Team, 2019). Details of the materials and methods are provided in Supplementary Material.

## 3. Results

### 3.1. Characteristic FTIR spectra of seagrass sediments

The FTIR sum absorbance spectrum of all the samples and its second derivative show the strongest absorbance for the bands in the region 400–1500 $cm^{-1}$. The strength of these absorption bands could be attributed to several inorganic and organic compounds which have multiple overlapped regions (Fig. 2). Such degree of overlapping makes the interpretation of FTIR spectra very complex and without the PCA, it would be almost impossible to explain the main differences between the FTIR spectra of the sediment samples.

Table S2 presents the band assignments of the selected peaks. Peaks from 400 to 1200 $cm^{-1}$ could be associated with the stretching vibration mode of the Si—O bond from silicates, including quartz and feldspar (Matteson and Herron, 1993; Margenot et al., 2017). Peaks around 1100 $cm^{-1}$, appearing together with peaks near 800 $cm^{-1}$, can be associated to the presence of biogenic silica (Meyer-Jacob et al., 2014; Sackett et al., 2015; Vogel et al., 2016). At the same region of Si—O bonds in minerals, vibrations could also be attributed to C—H out of plane bending and C—O stretching likely corresponding to aromatics and polysaccharides (Margoshes and Fassel, 1955; Giovanela et al., 2004; Wissel et al., 2008; Benito-González et al., 2019). The largest absorptions occur at ~1400 and 874 $cm^{-1}$. The co-occurrence of bands at 711, 855, 874, 1400–1500, ~1800, ~2500 $cm^{-1}$ can be associated to the vibration of carbonate ions (Tatzber et al., 2007; Bruckman and Wriessnig, 2013; Meyer-Jacob et al., 2014). Absorption bands along the region 1400–1500 $cm^{-1}$ could also correspond to diverse vibrations from multiple organic compounds, such as aliphatic chains, phenols, amides and aromatics (e.g. Giovanela et al., 2004; Gorgulu et al., 2007; Enev et al., 2014; Plis et al., 2014). Other bands that could also be linked to pure carbonates are ~2900 and ~ 3000 $cm^{-1}$, although they are even less characteristic because of their overlapping with the $CH_2$ stretching vibration of aliphatic components (Bruckman and Wriessnig, 2013; Plis et al., 2014). Peaks from 3400 to 3700 $cm^{-1}$ could be linked to O—H stretching and bending vibration, indicating the presence of clay minerals (Margenot et al., 2017). However, this region also overlaps with organic compounds, specifically to O—H and N—H stretching vibration modes from polysaccharides and proteins (Wissel et al., 2008). The only organic compounds that do not overlap with any minerogenic components are mainly proteins and also phenols, vibrating at 1653 and 1688 $cm^{-1}$, due to the vibration modes of C═O stretching and NH bending. These bands have been observed in seagrass tissues using FTIR (Rengasamy et al., 2011; Plis et al., 2014; Benito-González et al., 2019). Several peaks between 2920 and 2980 ($CH_2$ stretching vibration of aliphatic components; e.g. Wissel et al., 2008; Plis et al., 2014) do not overlap either with inorganic compounds.

### 3.2. Principal component analyses

Coast of Andalusia

The three components extracted by $PCA_{AND}$, accounted for 84% of the total variance, of which $PC1_{AND}$, $PC2_{AND}$, and $PC3_{AND}$ explained a 70%, 9% and 5%, respectively (Fig. 3). The assignment of FTIR-ATR wavenumbers to specific compounds was based on available literature and can be found in Table S2.

The first principal component ($PC1_{AND}$) is characterised by moderate-to-high positive loadings corresponding to silicates, including clay minerals (Si, Ti, Fe, and absorbances at 423, 469, 672, 693, 751, 798, 906, 3399 to 3700 $cm^{-1}$ wavenumbers), and to diverse organic compounds, mainly aliphatics, such as lipids, nitrogen-containing compounds (aminoacids/proteins), and polysaccharides (1653, 1688, 1794, 2280–2521, 2840–3000, 3399 and 3570–3700 $cm^{-1}$), likely in the form of organo-clay complexes. On the other hand, $PC1_{AND}$ has moderate-to-high negative loadings linked to carbonates (Ca, 711, 855, 874, and 1401 to 1511 $cm^{-1}$) but also to lignin-like organic structures including polysaccharides, phenols, and aromatic hydrocarbons (S, OM, 1032–1164, 1448–1511 $cm^{-1}$; Fig. 3 and Table 2). $PC2_{AND}$ showed moderate-to-high positive loadings corresponding to polysaccharides (OM, seagrass COM, S, 1032–1164 $cm^{-1}$) and most likely to biogenic silica (Si, Mn, 777, 798, 1032–1112 $cm^{-1}$). $PC2_{AND}$ had negative loadings at absorbances mostly associated with carbonates (Ca, 711, 855, 874, 1401–1511, 1794 $cm^{-1}$), but also with silicates (Ti, K, Fe, 531 $cm^{-1}$), TSI, and NHT $cm^{-1}$ (Fig. 3 and Table 2). $PC3_{AND}$ showed positive loadings corresponding again to silicates (Ca, Si, K, 469, 531, 693, 751, 777, 798, 982–1082 $cm^{-1}$) and to climatic variables (NHT, TSI, NAO). $PC3_{AND}$ negative loadings are indicative of a mix of organic matter compounds, more specifically, aromatics, polysaccharides, proteins, and lipids, likely deriving from seagrass tissue (OM, seagrass COM, 711, 874, 1401, 1794, 1653, 2521

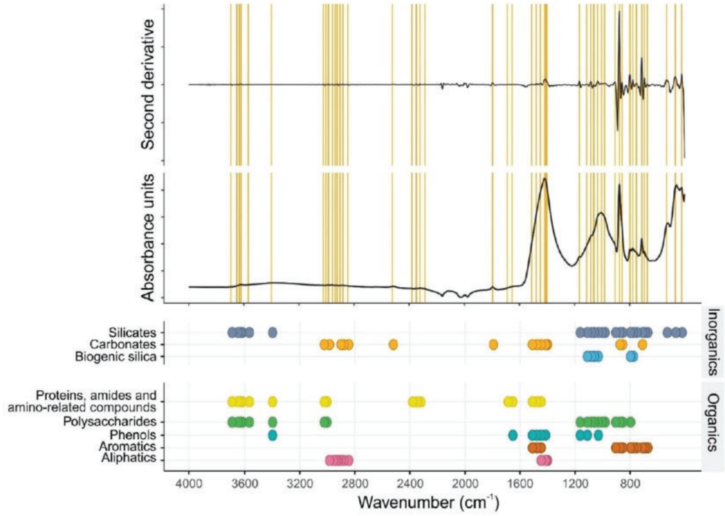

**Fig. 2.** Second derivative sum spectrum and FTIR absorbance sum spectrum of seagrass sediments. Vertical yellow lines indicate the peaks selected mainly based on the second derivative sum spectrum. Coloured circles below indicate the bands assignments for main components determination. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cm$^{-1}$). Iron, Mn, and S showed negative loadings as well in PC3$_{AND}$ (Fig. 3 and Table 2).

*Cabrera Island*

The two components extracted by PCA$_{CAB}$, accounted for 77% of the total variance, of which PC1$_{CAB}$ accounted for 65% and PC2$_{CAB}$ for 12% (Fig. 4).

The first principal component (PC1$_{CAB}$) is characterised by high positive loadings linked to aliphatics, such as lipids, and proteins but also polysaccharides (1794, 2286–3023, 3568–3700 cm$^{-1}$). Positive loadings of PC1$_{CAB}$ could also be linked to carbonates (Ca, 1794, 2521–2900, 2985, 3023 cm$^{-1}$) and clay minerals (Si, 3568–3693 cm$^{-1}$). PC1$_{CAB}$ showed negative loadings that could correspond to both silicates and aromatics and polysaccharides (OM, $\delta^{15}$N, Br, Cl, Fe, K, Ti, 423, 469, 531, 672, 693, 751, 777, 798, 906, 982 cm$^{-1}$ and several absorbances from 1004 to 1112 cm$^{-1}$; Fig. 4 and Table 2). PC2$_{CAB}$ showed positive loadings for variables related with carbonates and silicates (711, 798, 855, 906, 982, 1511 cm$^{-1}$, as well as, Fe, Si, Ti and Ca) while negative loadings would correspond to organic compounds, mainly proteins, carbohydrates, phenols, and lipids (OM, Br, Cl, S, $\delta^{15}$N, 1401–1416, 1653, 1688, 2845–3399 cm$^{-1}$), and to climate variables (NHT and TSI; Fig. 4 and Table 2).

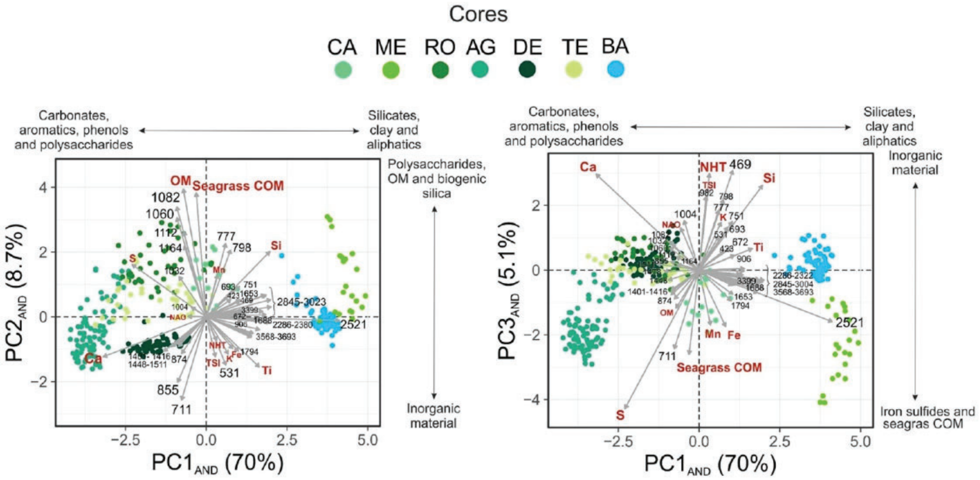

**Fig. 3.** Biplots for the FTIR peaks together with explicative variables from the cores along the Andalusian coast (PCA$_{AND}$): content of organic matter (OM), content of coarse organic matter from the seagrass (Seagrass COM), XRF-measured elements (Al, Fe, Si, Ti, K, Mn, Ca, Cl, S), Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009) and Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013).

**Table 2**
Factor loadings of the FTIR absorbances and rest of proxies used in PCA. Numbers in bold indicate peaks with the highest factor loadings. Numbers in bold and italic indicate peaks with moderate factor loadings. OM: organic matter content; Seagrass COM: organic material from seagrass (>2 mm); TSI: Total Solar Irradiance (Vieira et al., 2011); NAO: North Atlantic Oscillation (a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009); NHT: Northern Hemisphere Temperature (Kobashi et al., 2013).

| Variance explained | Andalusia | | | Cabrera | |
|---|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC1 | PC2 |
| | 70% | 8.7% | 5.1% | 64.8% | 12.5% |
| 423 | ***0.07*** | 0.05 | 0.05 | **−0.15** | 0.02 |
| 469 | **0.10** | 0.04 | **0.29** | **−0.28** | 0.05 |
| 531 | 0.06 | **−0.14** | **0.10** | **−0.26** | 0.04 |
| 672 | ***0.09*** | 0.00 | 0.06 | **−0.09** | 0.02 |
| 693 | ***0.08*** | ***0.08*** | **0.12** | **−0.09** | 0.05 |
| 711 | ***−0.07*** | **−0.24** | **−0.23** | −0.01 | **0.10** |
| 751 | **0.10** | ***0.09*** | **0.14** | ***−0.08*** | 0.04 |
| 777 | 0.06 | **0.21** | **0.17** | **−0.10** | 0.06 |
| 798 | ***0.07*** | **0.19** | **0.20** | **−0.09** | ***0.09*** |
| 855 | ***−0.08*** | **−0.19** | 0.02 | 0.06 | **0.14** |
| 874 | ***−0.07*** | **−0.11** | ***−0.08*** | 0.04 | −0.01 |
| 906 | **0.10** | −0.01 | 0.04 | **−0.19** | **0.11** |
| 982 | 0.02 | 0.01 | **0.21** | **−0.28** | ***0.08*** |
| 1004 | −0.04 | 0.03 | **0.14** | **−0.25** | 0.06 |
| 1032 | ***−0.08*** | **0.12** | 0.07 | **−0.26** | 0.05 |
| 1060 | ***−0.08*** | **0.28** | 0.06 | **−0.19** | 0.04 |
| 1082 | ***−0.08*** | **0.32** | 0.08 | **−0.15** | 0.06 |
| 1112 | −0.06 | **0.24** | 0.04 | ***−0.08*** | 0.03 |
| 1164 | −0.06 | **0.20** | 0.02 | 0.06 | 0.06 |
| 1401 | ***−0.08*** | ***−0.08*** | ***−0.07*** | 0.02 | **−0.17** |
| 1410 | ***−0.08*** | ***−0.08*** | −0.06 | −0.03 | **−0.14** |
| 1416 | ***−0.08*** | ***−0.08*** | −0.06 | −0.03 | **−0.12** |
| 1448 | ***−0.09*** | ***−0.08*** | −0.03 | 0.01 | −0.01 |
| 1478 | **−0.10** | ***−0.09*** | 0.00 | 0.00 | 0.06 |
| 1511 | **−0.12** | **−0.10** | 0.02 | −0.01 | **0.09** |
| 1653 | **0.10** | 0.05 | ***−0.07*** | −0.05 | **−0.14** |
| 1688 | **0.15** | −0.01 | −0.05 | 0.06 | **−0.10** |
| 1794 | **0.09** | **−0.10** | **−0.09** | **0.11** | −0.02 |
| 2286 | **0.18** | −0.02 | −0.03 | **0.09** | −0.02 |
| 2322 | **0.18** | −0.01 | −0.03 | **0.09** | −0.02 |
| 2348 | **0.17** | −0.01 | −0.03 | **0.09** | −0.03 |
| 2380 | **0.17** | −0.01 | −0.03 | **0.09** | −0.03 |
| 2521 | **0.38** | −0.01 | **−0.15** | **0.10** | −0.03 |
| 2845 | **0.18** | 0.05 | −0.05 | **0.15** | ***−0.08*** |
| 2881 | **0.17** | 0.06 | −0.06 | **0.15** | ***−0.08*** |
| 2902 | **0.17** | 0.06 | −0.04 | **0.14** | ***−0.09*** |
| 2922 | **0.10** | 0.02 | −0.04 | **0.12** | ***−0.08*** |
| 2937 | **0.11** | 0.02 | −0.03 | **0.12** | ***−0.08*** |
| 2955 | **0.16** | 0.02 | −0.05 | **0.13** | ***−0.07*** |
| 2985 | **0.17** | 0.01 | −0.05 | **0.13** | ***−0.07*** |
| 3004 | **0.19** | 0.03 | −0.03 | **0.12** | ***−0.07*** |
| 3023 | **0.13** | 0.03 | −0.01 | **0.12** | ***−0.08*** |
| 3399 | **0.10** | 0.01 | −0.04 | −0.03 | **−0.17** |
| 3568 | **0.14** | −0.05 | −0.04 | ***0.07*** | −0.05 |
| 3619 | **0.13** | −0.06 | 0.00 | ***0.07*** | −0.02 |
| 3632 | **0.13** | −0.05 | 0.00 | ***0.07*** | −0.02 |
| 3650 | **0.12** | −0.05 | −0.01 | **0.09** | −0.02 |
| 3693 | **0.15** | −0.04 | −0.03 | **0.10** | −0.02 |
| Si | **0.18** | **0.19** | **0.24** | **0.15** | **0.19** |
| S | **−0.21** | **0.15** | **−0.40** | 0.02 | **−0.20** |
| Br | – | – | – | **−0.16** | **−0.45** |
| Cl | – | – | – | ***−0.08*** | **−0.29** |
| K | 0.06 | **−0.11** | **0.14** | ***−0.08*** | **−0.10** |
| Ca | **−0.30** | **−0.11** | **0.27** | **0.34** | **0.39** |
| Ti | **0.15** | **−0.14** | 0.06 | ***−0.07*** | **0.18** |
| Mn | 0.03 | **0.12** | **−0.16** | – | – |
| Fe | ***0.08*** | **−0.09** | **−0.16** | **−0.11** | **0.28** |
| OM | ***−0.07*** | **0.37** | **−0.11** | ***−0.08*** | **−0.10** |
| Seagrass COM | −0.03 | **0.35** | **−0.24** | – | – |
| $\delta^{13}C$ | – | – | – | 0.04 | −0.06 |
| $\delta^{15}N$ | – | – | – | ***−0.07*** | **−0.15** |
| TSI | 0.03 | **−0.11** | **0.23** | 0.00 | **−0.10** |
| NAO | −0.05 | 0.00 | **0.12** | 0.00 | −0.03 |
| NHT | 0.03 | ***−0.07*** | **0.28** | 0.00 | **−0.16** |

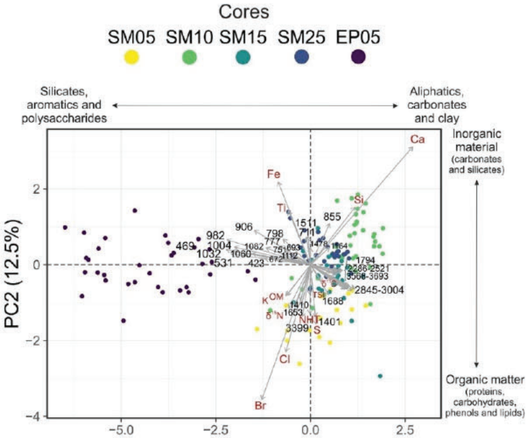

**Fig. 4.** Biplot for the FTIR peaks together with explicative variables from the cores retrieved in Cabrera Island ($PCA_{CAB}$): content of organic matter (OM), carbon and nitrogen stable isotopes, XRF-measured elements (Al, Fe, Si, Ti, K, Cl, Ca and Br), Total Solar Irradiance (TSI, Vieira et al., 2011), Index of North Atlantic Oscillation (NAO, a composite from Hurrell, 2003; Olsen et al., 2012 and Trouet et al., 2009) and Northern-Hemisphere Temperature (NHT, Kobashi et al., 2013).

### 3.2.1. Spatial patterns of PC scores

The box-plot of the component scores of $PCA_{AND}$ (Fig. 5A) showed some clear differences among cores. Cores located in the Mediterranean Andalusian side (AG, TE, DE) had lower scores in $PC1_{AND}$ than those situated at the Alboran Sea (ME, CA, BA), except for RO, one of the two stations situated near the Mediterranean-Alboran Sea limit. There is also a spatial gradient for $PC2_{AND}$ scores, although not as clear as in $PC1_{AND}$, with cores located to the east (DE, AG, BA, TE) showing lower scores. ME and AG had the highest scores for $PC3_{AND}$ while CA had medium values and RO, DE, BA, and TE had the lowest.

The box-plot of the $PCA_{CAB}$ scores (Fig. 5B) showed a clear difference between bays for $PC1_{CAB}$, with EP05 having lower scores than SM cores. SM10 had the highest PC1 scores, higher than the rest of the cores from the same bay. As for $PC2_{CAB}$ scores, SM05 had lower scores than the rest, while SM10 and SM25 had the highest mean values.

### 3.2.2. Temporal trends of PC scores

For every principal component, we found strong and significant positive relationships between the long-term temporal stability and the mean score value of each core in both areas, Cabrera and Andalusia (Fig. 6A and B).

Andalusia principal components scores showed no clear or common temporal trend among cores for $PC1_{AND}$ and $PC2_{AND}$ (Fig. 7A). $PC2_{AND}$ showed recent (over the last one or two centuries) temporal trends towards negative scores in CA, ME, and RO, while BA, AG and TE, showed recent temporal trends towards positive values. $PC3_{AND}$ showed recent temporal trends towards positive scores since ~100–50 cal. yr BP (AD ~1850–1900), trends more or less conspicuous, in every core. In cores reaching ages beyond 600 cal. yr BP (RO, AG, DE, TE), overall lower scores values of $PC3_{AND}$ were observed from ~150 to 650 cal. yr BP.

$PCA_{CAB}$ scores temporal trends were very variable. They did not show any clear common trend among cores for any of the principal components (Fig. 7B). SM10 had temporal trends towards negative score values for $PC1_{CAB}$ and $PC2_{CAB}$, especially for the last 400 years. Slighter temporal trends, also towards negative values, were observed at SM15 for $PC1_{CAB}$ and $PC2_{CAB}$ over the last 1800 years. SM05 and

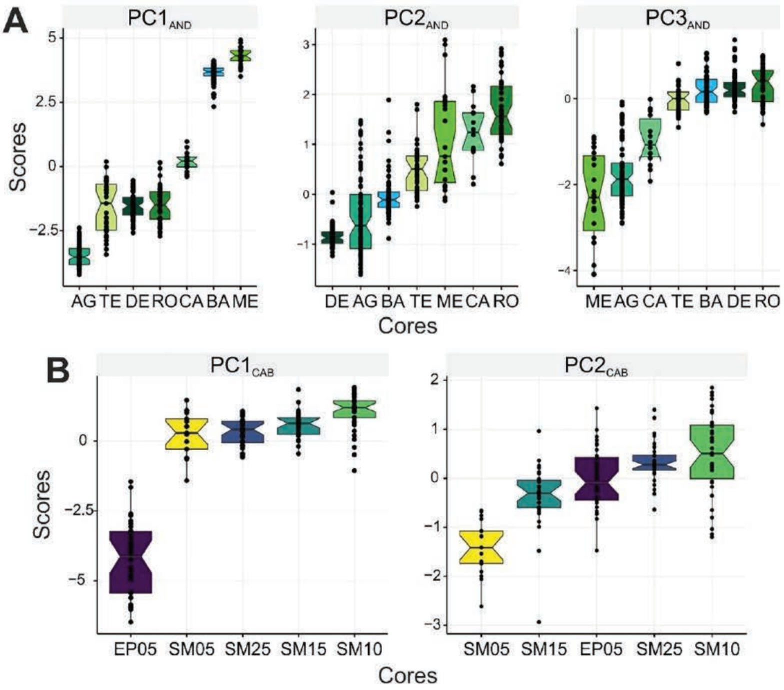

**Fig. 5.** Boxplot of the principal components (PC) scores for every core along the Andalusian coast –AND– (A) and from the Cabrera Island –CAB– (B). Boxplots are sorted by median value from the lowest to the highest.

EP05 had noisier trends, although with an overall tendency also towards negative values for $PC2_{CAB}$ over the last centuries.

## 4. Discussion

### 4.1. Terrestrial influence on marine production and OM preservation

$PC1_{AND}$ likely indicates the degree of aliphaticity (positive loadings) versus aromaticity (negative loadings) of the humic sediment material. This could be related to the composition of the main source materials (Rashid, 1985; Giovanela et al., 2004), with seagrass-derived OM corresponding to negative loadings and algae-derived OM associated to positive loadings. Moreover, the sedimentary environment prevailing at the time of deposition, which is closely linked to the living communities in the overlying water column, also influences the OM preservation (Schmidt et al., 2011) and hence the relative content of aliphatic and aromatic compounds.

In Andalusia, $PC1_{AND}$ positive loadings are indicative of meadows growing on terrigenous sediments with accumulation of lipids, nitrogen-containing compounds and polysaccharides, highly aliphatic compounds abundant in marine algal-derived OM (Giovanela et al., 2004; Mecozzi et al., 2009; Villacorte et al., 2015). Seagrasses tissues have a low content of nitrogen (1–3%; Duarte, 1990), so they are less likely to significantly contribute to the sediment nitrogen compounds. Significant seagrass losses and higher algal growth (macro- and micro-), deriving in an increased accumulation of allochthonous carbon from algae and microbes in seagrass sediments, usually occur in meadows influenced by terrigenous runoff, due to increased water turbidity and nutrient concentrations (Ralph et al., 2006; Macreadie et al., 2012; Liu et al., 2016; Mazarrasa et al., 2017a). FTIR absorbances also indicated anaerobic sediment conditions, given the abundance of carbonyl groups (C=O ~$1670–1790\,cm^{-1}$), effectively preserved under low-oxygen sediments (Rashid, 1985a), and clay, likely from continental runoff discharges, reducing sediment porosity and oxygenation, and maintaining a low redox potential. Clay minerals can also form organo-clay complexes, retarding the degradation of organic matter (Baldock and Skjemstad, 2000). These sediment conditions would help in the accumulation of aliphatics and nitrogen-rich compounds, which are otherwise preferentially degraded in aquatic environments (Derenne and Largeau, 2001; Tremblay et al., 2011). On the other side, negative loadings correspond to meadows growing on carbonate sediments less influenced by terrestrial inputs and where *P. oceanica* is very likely the primary OM source, due to the abundance of its main structural compounds: aromatics, phenolics, lignins, and also polysaccharides (Kaal et al., 2016). Therefore, $PC1_{AND}$ scores along the cores could indicate relative changes of the two main primary producers in a seagrass meadow: algae and seagrass, as well as of sedimentary conditions, thus, taking into account that both factors are probably not independent from each other.

This interpretation is consistent with the almost perfect division of $PC1_{AND}$ scores between cores located at the Alboran (CA, ME, RO, BA) and Mediterranean seas (AG, DE, TE; Fig. 5A), given that Alboran waters are richer in nutrients and phytoplankton than Mediterranean waters (Muñoz et al., 2015; del Carmen García-Martínez et al., 2019). A similar component to $PC1_{AND}$ is reconstructed in the Cabrera Island, although the organic compounds involved under similar environments are not the same, reflecting clear differences between study areas. $PC1_{CAB}$ would be related to a gradient between marine production, higher in Santa Maria Bay (SM), and terrestrial inputs, higher in Es Port Bay (EP), a closed bay. A higher delivery of terrestrial material in EP is coherent with the occurrence of the main pluvial network discharges in EP (Rodríguez-Perea and Servera, 1993). Under moderate terrestrial

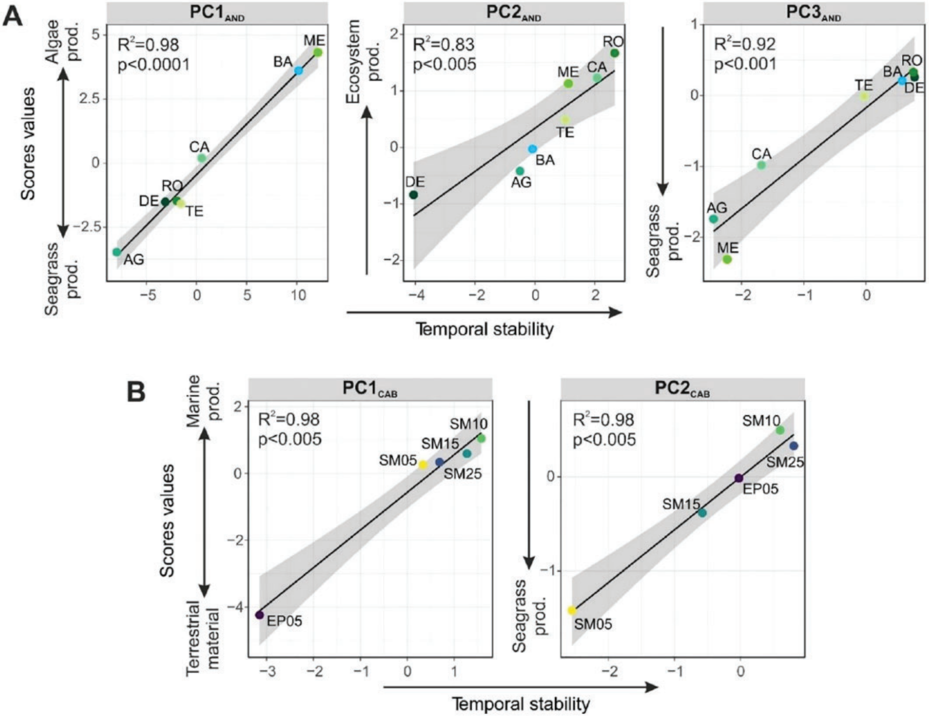

**Fig. 6.** Relationships between principal components (PC) temporal stability and level of mean score value of that component for every core in Andalusia –AND– (A) and Cabrera Island –CAB– (B). Black lines indicate a regression line and grey areas are prediction intervals. Labels next to points indicate the code of the core.

inputs (EP), Cabrera meadows sediments showed a higher abundance of polysaccharides and aromatics, while in Andalusia, under higher terrestrial inputs, the main organic compounds were aliphatics, lipids and proteins. Higher OM degradation rates may explain the lower content of aliphatics under terrestrial influence in Cabrera sediments. Holmer et al. (2003) reported high anaerobic degradation rates in EP due to the combination of high OM accumulation and more carbonate content as compared to coastal mainland meadows. Hence, the more labile aliphatics would be further consumed in EP and sediments would get enriched in aromatics and polysaccharides terrestrial compounds, more difficult to degrade. The aliphatics predominance in SM points to an elevated phytoplanktonic input in the sediments of this bay. The sediment carbon isotope ratios also pointed to this, as they showed depleted values of $\delta^{13}C$ ($-20.6 \pm 1.7$‰, Table S3), close to the signal characteristic of seston (e.g. ~$-22 \pm 2$‰, Papadimitriou et al., 2005). It seems that seagrass meadows in Cabrera have higher sestonic inputs than in Andalusian meadows, where sediment $\delta^{13}C$ is closer to that of seagrass material ($-16 \pm 2$‰, Table S3), most likely because Cabrera meadows are located in bays with longer water residence times would favour seston sedimentation (4–15 days in bays of Cabrera -Marbà et al., 2002; Orfila et al., 2005- while ~<1 day in the open meadows of Andalusia). A higher phytoplanktonic contribution in Cabrera Island meadows compared to others Balearic meadows was already observed by Holmer et al. (2004).

### 4.2. Ecosystem and seagrass production

$PC2_{AND}$, $PC3_{AND}$ and $PC2_{CAB}$ could be all related to processes of marine community or seagrass production. Positive loadings of $PC2_{AND}$ are likely linked to the whole community production since they include total OM content, seagrass COM, biogenic silica and polysaccharides, ubiquitous and abundant compounds in marine photosynthetic organisms (Burdige, 2006). Manganese is typically associated with biogenic silica, as a surface coating (Ingall et al., 2013). Therefore, its positive loading quite close to the silica signal in $PC2_{AND}$ suggests a biogenic origin for both accumulations (Fig. 3). Polysaccharides can be preferentially degraded in marine sediments (Arnosti et al., 1994; Mckew et al., 2013), so its accumulation independent of the clay content is likely indicative of high primary production. Moreover, $PC2_{AND}$ scores along the cores did not show clear common degradation trends of polysaccharides with ageing (except maybe in AG and BA where the recent sediment layers have a higher content of polysaccharides, Fig. 7A).

Negative loadings of $PC3_{AND}$ are likely indicative of seagrass production, with a mix of organic compounds including aromatics, carbohydrates, phenols, proteins, and lipids that are found in *P. oceanica* tissues (Kaal et al., 2016). Seagrass production seems to be closely linked to sediment conditions that enhance iron-sulfides precipitation, given the high negative loadings for Fe, S, and Mn (Fig. 3 and Table 2). These sediment conditions seem to be favoured under certain climatic conditions that will be later discussed.

In coastal vegetated marine sediments, sulfate reduction is the main pathway of organic matter mineralisation due to the prevailing geochemical conditions (anaerobia, high availability of organic matter, and dissolved sulfates; Howarth, 1984). The observed coupling between sulfate reduction rates and the seagrass photosynthetic activity led to the hypothesis that plant root exudates, providing labile organic carbon, fuelled sulfate-reducing bacteria (Oenema, 1990; Nielsen et al., 2001;

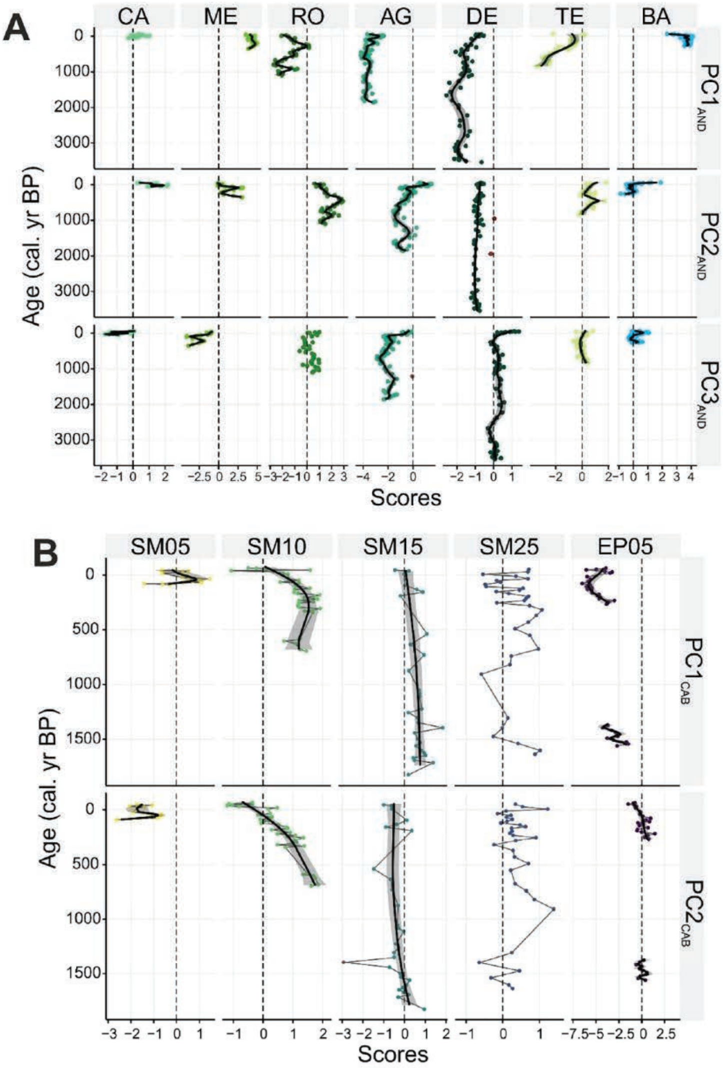

**Fig. 7.** Depth records of the principal components (PC) scores obtained in PCA for every core along the coast of Andalusia –AND– (A) and from the Cabrera Island –CAB– (B). Abbreviations above records (CA, ME…) correspond to the code of the core. Black solid lines indicate the fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant ($p < 0.05$) trends are shown. Red points were considered outliers and not included in GAM models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Otero et al., 2014). Sulfides have phytotoxic properties to seagrasses, negatively affecting their production and growth and increasing their mortality (Carlson et al., 1994; Holmer and Hasler-Sheetal, 2014). These negative effects were observed in seagrasses growing in contrasting sediments (Holmer and Kendrick, 2013), although meadows in carbonate sediments show higher sensitivity to anoxia and sulfides due to low iron contents (Holmer et al., 2003; Ruiz-Halpern et al., 2008).

Besides the classic limitation of iron for growth (Moore et al., 2013; Bristow et al., 2017), iron can further limit seagrass production through sulfides buffering. Iron has a key role re-oxidising and burying a significant part of sulfides compounds as iron-sulfide, such as pyrite ($FeS_2$), which reduces plant exposure to sulfide and can stimulate seagrass growth rates (Chambers et al., 2001; Holmer et al., 2005; Marbà et al., 2007, 2008; Ruiz-Halpern et al., 2008; Devereux et al., 2011; Xu et al., 2019; Li et al., 2020). The presence of iron sulfides, mainly pyrite, has been observed in sediments of coastal vegetated ecosystems including seagrass meadows (Holmer et al., 2006; Ku et al., 2008; Ferreira, 2010). Pyrite formation in marine ecosystems is primarily limited by the amount and reactivity of OM inputs into the sediment but also by the abundance and reactivity of detrital iron minerals (Berner et al., 1985; Otero et al., 2014). Therefore, a higher input of iron (probably together with other nutrients) to seagrass meadows could ameliorate the adverse effects of sulfide stress and allow elevated seagrass production and OM burial. Higher seagrass production and OM burial would enhance sulfate reduction rates and, together with the higher iron availability, pyrite formation would also increase, explaining the positive correlation between seagrass COM, Fe and S found in this study. The high loading of Mn together with Fe and S could be a result of coprecipitation of Mn (II) with iron sulfides in anoxic-sulfidic environments (e.g. Otero and Macias, 2003).

In Cabrera, $PC2_{CAB}$ is most likely indicating changes in the seagrass production. Most of the FTIR absorbances loading in this component are associated with seagrass compounds (carbohydrates, phenols, lipids, Fig. 4), which also appear in $PC3_{AND}$, its equivalent component in the coastal mainland cores. The core with the most negative scores for $PC2_{CAB}$ is SM05, which had the highest amount of seagrass detritus, as observed during laboratory processing - reinforcing the $PC2_{CAB}$ interpretation. A difference between the seagrass production between Cabrera and Andalusia, as reconstructed here, is the fact that seagrass production in Cabrera is not related to iron. This was not expected given the low content of iron in carbonate sediments. However, our results are consistent with previous research in the area showing that iron additions did not stimulate seagrass growth in SM and did not completely eliminate nutrient limitation in neither of two the bays studied here (Holmer et al., 2005). This fact, together with the positive loading found for $\delta^{15}N$ in the seagrass production component ($PC2_{CAB}$, Fig. 4), suggests that nitrogen could be the main limiting nutrient in meadows around the Cabrera Island.

The highly significant correlation between current mean seagrass shoot densities and their most recent $PC3_{AND}$ and $PC2_{CAB}$ scores values (approximately from 2000 to 2018; Fig. S3), reinforces our interpretation of negative scores from both principal components being related with seagrass production. Mean seagrass shoot densities for each study site were calculated from collected literature data covering diverse periods between 2004 and 2018 for Andalusia and between 2000 and 2007 for Cabrera (Table S4). All reconstructed ecosystem and seagrass production processes are negatively correlated to inorganic terrigenous elements. This does not necessarily indicate higher terrestrial runoff. Instead, it is more likely related to a dilution effect in which less seagrass production implies less OM and higher inorganic material content.

### *4.3. Climate influence on long-term nutrient availability and seagrass production*

Seagrass production in Andalusia was correlated with higher sediment concentration of iron sulfides and anticorrelated with global climate variables ($PC3_{AND}$ in Fig. 3), indicating that seagrass production is enhanced during periods of lower solar irradiance and air temperature and negative NAO phases. Present and past climate in southern Iberia is related to the NAO index, mainly regarding changes in precipitation, with negative NAO phases coinciding with wetter periods and enhanced fluvial discharges (Trigo et al., 2004; Liquete et al., 2005; Nieto-Moreno, 2012; Benito et al., 2015; Sánchez-López et al., 2016). These terrestrial discharges would supply nutrients, including iron, which would buffer sulfides and seagrass production would ultimately increase. Ausin et al. (2014) reported a positive correlation between periods of increased paleoproductivity and negative NAO phases in the Alboran Sea. They hypothesised that during negative NAO phases, atmospheric conditions derived in increased seawater vertical mixing and intensified upwelling conditions. Prevalent upwelling conditions during negative NAO phases would also supply nutrients and iron into the coastal area.

Global climate variables - air temperature and, to a lesser extent, solar irradiance - are also correlated with seagrass production in Cabrera ($PC2_{CAB}$ in Fig. 4). This relationship could also be linked to changes in local/regional climate, and hence, in terrestrial inputs, which could cause changes in nutrient availability. However, unravelling the exact mechanism is currently a complex endeavour because local climate reconstructions did not find correlations with global climate variables around the Balearic Islands (Cisneros et al., 2015).

### *4.4. Spatial patterns and temporal stability*

Along the mainland coast, the main source of OM was found to be algal in two *P. oceanica* meadows (CA, ME) and in the only *C. nodosa* meadow (BA) of this study (Fig. 5A). In these meadows, the OM source has barely changed within the last centuries (Fig. 6A). A higher contribution of algal vs seagrass material in CA and ME is consistent with their location in the western side of the Andalusian coast, receiving higher river water discharges due to their wetter climate and being closer to areas subjected to periodic upwelling of deeper waters with high nutrient concentrations (Sarhan et al., 2000; Liquete et al., 2005; Macías et al., 2007; CAGPDS, 2014). BA is a meadow located under the influence of a Mediterranean river with the highest capacity in Andalusia (Andarax, transporting more sediment per water discharge, Liquete et al., 2005), and with a strong torrential character. This area is therefore subjected to sudden and high sediment discharges, very unstable environmental conditions under which *P. oceanica* cannot survive and it is hence replaced by *C. nodosa*. *C. nodosa* is an opportunistic species with a higher capacity of recovery and to acclimate to environmental variability (e.g. Marbà et al., 1996; Cancemi et al., 2002; Olesen et al., 2002; Kilminster et al., 2015). On the other hand, meadows with higher seagrass than algal production are those located more to the east (AG, DE, and TE; Fig. 5A), areas where the climate is more arid and water river discharges are much lower and irregular (Fernández Salas et al., 2015). The irregular terrestrial influence may explain the higher variability regarding changes in primary producers (Fig. 6A). The only exception to this geographical pattern was RO, situated a few miles westward from BA, but still near to the Alboran-Mediterranean limit, in a very shallow (1 m) *P. oceanica* barrier-reef.

In general, the higher the meadow ecosystem production ($PC2_{AND}$), the more to the west the meadow is located. An environmental gradient along the coast most likely related to the water nutrient availability gradient (with richer waters towards the west), which seems the main driver behind the ecosystem production. Moreover, ecosystem production showed more temporally stable dynamics in meadows with higher production, most probably because of more stable environmental conditions with less torrential terrestrial influence ($PC2_{AND}$ vs temporal stability in Fig. 6A). On the other hand, seagrass production level showed a negative relationship with its temporal stability, both in Andalusia and in Cabrera (Fig. 6A and B), which reveals a long-term trade-off between the stability and level of seagrass production. Similar trade-offs were also observed in temperate forest ecosystems (Albrich et al., 2018), as well as in agricultural systems (Deguines et al., 2014; Montoya et al., 2019). Meadows with lower stability may also have lower long-term resilience. The temporal dynamics of ecosystems with low resilience that approach a critical transition, show an increase in variance (Scheffer et al., 2015). Therefore, meadows with higher long-term stability in seagrass production, are likely to have higher resilience and resistance, being also easier for managers to maintain.

In the Cabrera Island, EP showed higher terrestrial inputs and lower marine production compared to SM ($PC1_{CAB}$, Fig. 5B), which is consistent with the higher discharge of the main pluvial network in EP (Rodríguez-Perea and Servera, 1993). Mazarrasa et al. (2017a) also reported a higher contribution of allochthonous carbon in EP compared to SM. Regarding the seagrass production in the island ($PC2_{CAB}$), SM05 stands out as the station with the highest seagrass production with deeper stations having lower production (except for SM10) (Fig. 5B). Lower seagrass production with water depth is a gradient widely described, related to reduced seagrass growth and production at physiological but mostly at structural levels (Dennison, 1987; Olesen et al., 2002; Collier et al., 2007; Enríquez et al., 2019).

### 4.5. *C. nodosa* compared to *P. oceanica* long-term dynamics

As for the long-term dynamics of the production of the *C. nodosa* meadow in this study (BA), our results point to a meadow that does not seem much different from some *P. oceanica* meadows. Seagrasses with smaller sizes tend to be less productive and have lower biomass (Duarte and Chiscano, 1999; O'Brien et al., 2018). However, the median score values of the reconstructed processes $PC2_{AND}$ and $PC3_{AND}$ for BA are within the range of other *P. oceanica* meadows (Fig. 5A). There are, therefore, some *P. oceanica* meadows showing lower levels of long-term production than *C. nodosa*. This means that the long-term community and seagrass production of this *C. nodosa* meadow are not the lowest as it was expected. In a compilation by Duarte and Chiscano (1999), *C. nodosa* showed almost 2-fold lower values of above and belowground production (1.3 and 0.2 g DW $m^{-2}$ $day^{-1}$, respectively) compared to *P. oceanica* (2.4 and 0.2 g DW $m^{-2}$ $day^{-1}$, respectively). However, other studies have reported higher values of leaf production for *C. nodosa* that are comparable to other seagrass species such as *P. oceanica* (Rismondo et al., 1997; Agostini et al., 2003; Cunha and Duarte, 2007; Terrados et al., 2006 and references therein; Sghaier et al., 2011). In our study, the main difference between the *C. nodosa* meadow and most of the *P. oceanica* meadows is related to the relative production of algae versus seagrass ($PC1_{AND}$ in Fig. 5A). The *C. nodosa* meadow shows a higher algal production relative to the seagrass compared to most of the *P. oceanica* meadows. This is in agreement with studies showing that the associated community of *C. nodosa* showed higher biomass of algal epiphytes compared to *P. oceanica* (Mazzella et al., 1998; Mabrouk et al., 2014). Another difference of the *C. nodosa* meadow is that it is the only seagrass meadow showing a clear tendency of recovery of its production since AD ~1950 after the overall seagrass decline along the Andalusian coast since AD ~1850 (Fig. 7A). This is likely indicative of the greater capacity of recovery of the *Cymodocea* genus compared to *Posidonia* spp. (O'Brien et al., 2018). However, the comparison between the two seagrass species is not balanced in our study, because we only investigated one core from a *C. nodosa* meadow so the results should not be extrapolated. Further studies aiming to elucidate the similarities and differences between the long-term dynamics of the seagrass species should include more cores from meadows dominated by smaller species.

### 4.6. Temporal trends

In general, $PC1_{AND}$, $PC2_{AND}$ and $PC1_{CAB}$ scores did not show common temporal trends throughout time (Fig. 7), which points to local factors as the main drivers of changes in primary producers and ecosystem production. However, the GAMs did show a clear common trend for $PC3_{AND}$, component related to seagrass production in Andalusia (Fig. 7A). More specifically, a decrease in seagrass production is observed in Andalusia since AD ~1850/1900, in line with the general seagrass decline trend since AD 1850, observed by Marbà et al. (2014). In cores reaching ages beyond 600 cal. yr BP (RO, AG, DE, TE), lower scores values of $PC3_{AND}$ (indicating higher seagrass production) were observed during the Little Ice Age (LIA; ~150 to 650 cal yr BP). Considering the anticorrelation between global climate variables and seagrass production ($PC3_{AND}$; Fig. 3 and Table 1), the long-term variability of seagrass production is most likely related to changes in global climate, although combined negative impacts of both local anthropogenic changes and global climate cannot be discarded, especially during the decrease of the last century.

Sea surface water temperatures (SST) in the Alboran Sea have been rising coeval with global warming, with a sharp and unprecedented SST increase since 150 cal. yr BP (AD ~1850, Fig. 8; Nieto-Moreno, 2012). Temperature rise can directly affect the performance of seagrasses, since they show high sensitivity to seawater warming, at physiological and population levels, decreasing their growth and even causing plant mortality (Mayot et al., 2005; Díaz-Almela et al., 2009; Marbà and Duarte, 2010; Collier and Waycott, 2014; Hendriks et al., 2017). The biogeochemical process closely related to long-term seagrass production according to our results in Andalusian seagrass meadows, sulfate reduction, is also enhanced by increased water temperature (Koch et al., 2007; Sanz-Lázaro et al., 2011). Since AD ~1950 there is also a trend towards more positive values of the NAO index and, as mentioned above, positive NAO phases in the Alboran Sea are linked with lower terrestrial discharges and upwelling events, limiting nutrient and iron availability to the seagrass meadows (Ausin et al., 2014; Sánchez-López et al., 2016). Therefore, the sediment buffering capacity of sulfides would be most likely surpassed during drier and warmer periods due to a higher accumulation of the phytotoxic sulfides and lower arrival iron inputs, further compromising the seagrass development. The LIA is evidenced as a colder and wetter period with higher riverine influence due to lower solar irradiance and lower NAO values (Nieto-Moreno, 2012; Oliva et al., 2018). A higher delivery of terrestrial material together with a higher frequency of upwelling events would have brought nutrients and iron into the coastal area stimulating seagrass production and explaining the negative $PC3_{AND}$ score values reached during the LIA (Fig. 8).

Previous studies showed that most of our study sites are currently experiencing interannual-decadal negative growth rates (CAGPDS, 2018). Our results indicate that this trend is likely to have already started around AD ~1850 along the mainland coast, moment when the sea also started to warm up, what would point to temperature as a key factor that affected seagrasses performance (Fig. 8). In contrast, long-term negative trends of seagrass production during the last centuries were not evident in our cores from Cabrera Island ($PC2_{CAB}$, Fig. 7B). However, recent studies have also shown current negative seagrass growth rates in this specific island of the Balearics, where seawater temperature rise was found to be a main driver (Marbà et al., 2005; Marbà and Duarte, 2010). This poses the question of why Cabrera meadows were not registering a long-term negative effect derived from global and seawater warming. It turns out that an SST reconstruction around the Balearic Islands did not show the centennial warming trend registered in the Alboran Sea since the industrialisation, although this could be a consequence of a much lower temporal resolution in the study of Cisneros et al. (2015). The western Alboran anticyclonic gyre showed a more intensive warming trend than Balearic waters in summer and autumn over the 1982–2012 period (Shaltout and Omstedt, 2014). We should also consider the role of negative anthropogenic effects along the coast of Andalusia where the population has been growing since ~1920 (Instituto de Estadística de Andalucía, 1999), while in Cabrera Island there has never been a permanent population of more than ~50 people (Frontera et al., 1993). In fact, the steepest decline reaching the lowest values of seagrass production is observed at DE, a meadow impacted by industrial discharges over the last decades (Moreno et al., 1999, 2001). The combined negative impacts of local anthropogenic changes and a plausible more acute seawater warming in the Alboran sea, could explain why declining trends started earlier in seagrass meadows along the coast of Andalusia. The fact that Andalusian meadows are close to the *P. oceanica* geographical range limit (Mateo Ramírez et al., 2016) likely made them more vulnerable and could have also played a role in their worse past and present state. Besides, these results also highlight the role of past conditions in driving the present dynamics of seagrass ecosystems. This legacy should be considered when trying to understand the current worse state of the Andalusian meadows, with lower population growth rates than in the Balearic Islands (Marbà et al., 2005). The influence of past disturbances has also been found to be a factor driving the contemporary dynamics of terrestrial forests (Herzschuh et al., 2016; Schurman et al., 2018).

Some previous studies have pointed to cumulative effects of multiple local impacts as the main or even unique causes behind *P. oceanica* loss, concluding that meadows may be recovered and managed through local actions (González-Correa et al., 2007;

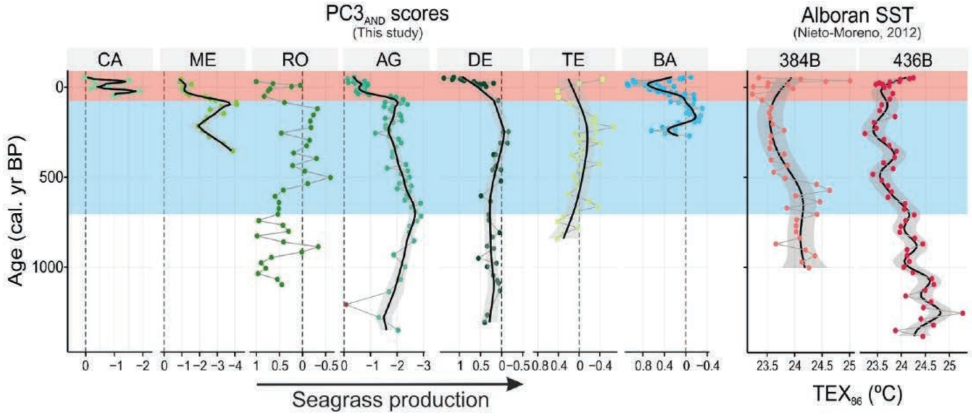

**Fig. 8.** Depth records of PC3$_{AND}$ scores obtained in PCA$_{AND}$ plotted together with Alboran sea surface temperature (SST) reconstructions (Nieto-Moreno, 2012). Abbreviations above records (CA, ME…) correspond to the code of the core. SST were based on archaeal isoprenoid tetraether membrane lipids, the TEX$_{86}$ index (Schouten et al., 2002). Light red area highlights the recent warming period observed in Alboran SST records and the light blue area indicates the Little Ice Age period. Positive scores of PC3$_{AND}$ are related to lower levels of seagrass production. Black solid lines indicate the fitted smooth functions of time (GAM models, formula = y ~ s(x)) and grey shaded regions are 95% point-wise confidence intervals. Only GAMs with significant ($p < 0.05$) trends are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Boudouresque et al., 2009; Guillén et al., 2013; Telesca et al., 2015). Our results add up to this discussion and indicate that even though seagrass regression seems spatially variable, it cannot be only ascribed to local causes. This would reinforce Marbà et al. (2014) pointing to both, widespread disturbances acting at a local scale and long-term global disturbances, as factors behind *P. oceanica* loss. Additionally, local and global causes of seagrass regression seem to have spatially different relative weights, and the effect of their combined action seems, at least, additive.

Taking into account that our long-term data point to climate warming as a major driver of seagrass production and that the Mediterranean Sea is expected to be one of the regions most affected by human-induced warming in the next decades (Giorgi, 2006; IPCC, 2013), we could expect most Mediterranean seagrass meadows to continue declining. This supports Jordà et al. (2012), who stated that seagrass declining trends due to higher temperatures were found to be ineludible even if other local anthropogenic pressures were entirely mitigated. However, this decline most likely will not be spatially homogeneous, with some seagrass meadows being more vulnerable and degraded at faster rates than others, such as those in the Alboran Sea. On the other side, the long-term impact of climate change is not so evident in the sedimentary record of meadows located in the Cabrera Island. Their location could be a refuge from climate change, and local actions could be more effective there. It should also be considered that most of our cores were extracted at shallow and intermediate water depths. Therefore, the long-term impact of climate change on the lower limit of the meadows, more vulnerable as they are closer to the compensation depth, is not being addressed in our study. In other words, the overall long-term impact of climate might have even been more acute in deeper areas.

### 4.7. Managing seagrass habitats considering their long-term dynamics

Our paleoecological approach has provided specific information about the long-term stability of seagrass production for each meadow and the more probable causes of long-term change at a regional scale. Long-term data of the seagrass life-history that can help design more targeted management and conservation plans (Kilminster et al., 2015). Our results also revealed a significant long-term trade-off between the level of seagrass production and its temporal stability. The seagrass production stability over long term scales could decrease if managers only follow the criteria of maximising the level of seagrass production. Therefore, this information about the long-term stability should be taken into account in seagrass conservation and management plans aiming to increase their resilience (Kilminster et al., 2015), especially under the increasingly unstable future scenarios.

Following Game et al. (2008) considerations, the optimal strategy of conservation in ecosystems that are likely to spend more time in a degraded state, such as meadows along the more anthropised Andalusian coast, is to protect low-risk sites. Along Andalusia, the lowest-risk sites would be those meadows in their eastern side, that seem more resilient given their overall higher long-term temporal stability. However, in areas where meadows are under less stress, such as meadows in the Cabrera Island, it is best to take actions in the locations with higher risk. In Cabrera, that would correspond to the currently more impacted EP Bay. To sum up, the effectiveness of managing at a local-scale would more likely not be equal everywhere, because local and global impacts seem spatially different. The long-term data provided by paleoecological reconstructions can help in identifying those areas where local management could be more efficient.

## 5. Conclusions

This work demonstrates that FTIR is a powerful and useful method for paleoreconstructions in seagrass meadows, which in combination with other geochemical proxies and the multi-core approach used here, has allowed to get insights into the long-term seagrass processes and their dynamics. Our findings revealed key ecosystem processes, most of them associated with production, and provided a regional perspective for these processes.

Our study provides more reliable baseline data, helps to assess the magnitude of seagrass regression as well as elucidating the long-term causes behind seagrass decline, which seem spatially variable. We observed a common regressive trend of seagrass production in meadows located along the southern coast of Spain since AD ~1850–1900. Seawater warming, together with local impacts due to a highly anthropised coast, may have had a combined negative influence in the long-term seagrass production along the mainland coast. This pattern is not observed in meadows around the Cabrera Island, which could be due to geographical differences in seawater warming, together with more pristine conditions and a more central position in the species geographic range (and thus, natural environmental conditions). Our reconstruction contextualizes and helps to understand the differences in current seagrass decreasing trends. The present worse state of seagrass meadows along the mainland coast may be linked to the legacy of more conspicuous negative effects derived from past seawater warming and human impact. Further studies would be needed to confirm and assess the magnitude of the spatial differences in the influence of climate change in seagrass meadows along the Mediterranean.

## CRediT authorship contribution statement

**Carmen Leiva-Dueñas:** Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Validation, Visualization, Writing - original draft, Writing - review & editing. **Antonio Martínez Cortizas:** Methodology, Data curation, Formal analysis, Writing - review & editing. **Nerea Piñeiro-Juncal:** Data curation, Formal analysis, Project administration, Writing - review & editing. **Elena Díaz-Almela:** Data curation, Formal analysis, Project administration, Writing - review & editing. **Jordi Garcia-Orellana:** Methodology, Data curation, Formal analysis, Writing - review & editing. **Miguel A. Mateo:** Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.142117.

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