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Memoria presentada por Jesús Villellas Ariño para optar al grado de Doctor por la Universidad de Barcelona.

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Doctorando	Directora de tesis	Tutor
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No puede impedirse el viento. Pero pueden construirse molinos

Proverbio holandés

A mis padres

Contents

Agradecimientos

Agradecimientos

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General Introduction

General Introduction

1. Widespread plants

Widespread and common species, those presenting large range sizes and high abundances, have traditionally received much less attention than rare and endemic ones in the ecology and conservation literature (Gaston 2011). The greater concern that scientists usually have about rare phenomena and taxa likely explains why the importance of widespread species has been so far overlooked. However, the interest in these organisms has increased in the last decade. Firstly, widespread taxa deserve attention because they are relatively rare in terms of number of species (Jaccard 1912, Preston 1948, Margules and Usher 1981), and because steady declines in abundance have been reported for a number of them (Gaston and Fuller 2007, Gaston 2010). In addition, their importance in macroecological patterns of species richness and species spatial turnover (e.g., Jetz and Rahbek 2002, Lennon et al. 2004, Pearman and Weber 2007), and in ecosystem structure and functioning (Smith and Knapp 2003, Solan et al. 2004, Bunker et al. 2005, Emery and Gross 2007, Polley et al. 2007, Gaston and Fuller 2008) is becoming increasingly recognized. On the other hand, many widespread species are invasive or alien (Stohlgren et al. 2011), and may have detrimental effects on host ecosystems. Hence, understanding the characteristics that allow widespread organisms to extend over large areas has a high interest from both theoretical and applied perspectives, especially if we consider the low phylogenetic signal shown by species' range sizes and thus the low predictability of range size (Gaston 2003).

The search for features characteristic of plant species with small *vs*. large distribution ranges is indeed common in the scientific literature (e.g., Fiedler 1987, Byers and Meagher 1997, Hegde and Ellstrand 1999, Walck et al. 2001, Brown et al. 2003, Köckemann et al. 2009). Some reproductive traits have been typically found in widespread plants in comparison with species of smaller range sizes, such as higher levels of sexual reproduction, higher reproductive output and/or higher dispersal abilities (Kunin and Gaston 1993, Kelly 1996, Byers and Meagher 1997, Murray et al. 2002, Lavergne et al. 2004). These results point to a higher capacity of colonization in widespread plants (Fiedler 1987, Lavergne et al. 2004), although some studies have found different patterns (Brown et al. 2003, Simon and Hay 2003). Integrative analyses combining different vital rates, and/or describing population dynamics are scarcer. Some studies comparing the overall performance of congener plants with similar habitats found higher growth rates and/or lower extinction risks in populations of widespread compared to rare species (Fiedler 1987, Münzbergová 2005), whereas another study reported no clear relationship between the range sizes and population growth rates of two perennial plants (Byers and Meagher 1997).

One of the most frequent hypotheses to explain the success of plants distributed over large areas is that they show much wider ecological niches (Brown 1984). For example, weeds are the paradigm of widespread organisms with tolerance to a broad range of environmental conditions (Baker 1974). A positive relationship between niche width and range size has also been found in the herbaceous flora of central England (Thompson et al. 1998) and in European tree species (Kolb and Diekmann 2005, Köckemann et al. 2009). Other studies, in contrast, have failed to find such relationship in plant taxa (Burgman 1989, Thompson and Ceriani 2003, Kolb et al. 2006), suggesting no consistent pattern. If widespread species truly show higher niche breadth, a high variability in their life-history and demographic traits with respect to biotic and abiotic conditions is expected. Some transplant experiments have reported such life-history adaptability across widespread plants' ranges (Joshi et al. 2001, Santamaría et al. 2003), but other studies found no higher variation in phenotypic traits in common than in rare species (Primack 1980). Genetic diversity could also contribute to the ecological breadth of plants, and several reviews have shown indeed a tendency towards higher genetic variation in widespread taxa (Hamrick and Godt 1996, Gitzendanner and Soltis 2000, Cole 2003), although two of them warned that generalizations might be problematic (Hamrick and Godt 1996, Gitzendanner and Soltis 2000).

2. Sources of variation in widespread plants

The literature shows some common attributes of widespread plants, although there are also numerous exceptions and contradictory results, as seen above. It seems that studies are often very specific and carried out over small spatio-temporal scales, which hinders a general understanding of demographic, life-history and genetic variation in widespread taxa. In fact, different biological characteristics may be affected by different processes throughout species' ranges. Environmental and geographical gradients, which are intimately associated, seem to be appropriate scenarios in which to analyze the possible causes and the magnitude of natural intraspecific variation (Gaston et al. 2008).

2.1. Spatio-temporal variation in environmental conditions

Environmental factors constitute major agents of divergence in plant traits. Many studies have shown indeed intraspecific variation in different life-history traits in relation with climate (Murray et al. 2004, Nakazato et al. 2008, Koenig et al. 2009), moisture (Schimpf 1977), length of the growing season (Johnson and Cook 1968, Winn and Gross 1993), soil properties (Treseder and Vitousek 2001, Braza et al. 2010) or biological interactions (Pajunen 2009). Environmental stress, which may be caused by some of these factors, is central in the ecology and evolution of plants (Grime 1977, Odum 1985, Nevo 2001, Callaway et al. 2002) and has been found to trigger intraspecific variation as well (e.g., Loreti and Oesterheld 1996, Hester et al. 1998, Scarano et al. 2002). In this context, studies across large latitudinal gradients are very useful, as they often provide the opportunity to analyze environmentally driven variation in life-history traits among populations (Moles and Westoby 2003, Gaston et al. 2008, De Frenne et al. 2011).

Temporal variability in environmental conditions is another key factor shaping life history and demographic performance (Stearns 1976, Tuljapurkar et al. 2003). In fact, temporal variation in vital rates, such as fecundity or survival, due to environmental fluctuations, usually reduces population performance in the long term (Lewontin and Cohen 1969, Gillespie 1977). However, very few studies have quantified the real effect of intraspecific differences in vital rates' variation on the differences in population growth rates (Davison et al. 2010). Thus, further research is needed to explore the consequences of temporal variation in plant performance, especially if we consider the predictions of increasing variability in climatic parameters with global warming (Karl and Trenberth 2003, Salinger 2005).

2.2. The position of populations within species' ranges

The central *vs*. peripheral position of populations within species' ranges should also be accounted for when analyzing intraspecific variability. Central and peripheral populations are indeed expected to differ in a number of demographic, life-history and genetic traits. For example, the abundant-centre model assumes that core populations will present higher densities than peripheral ones, because environmental conditions tend to be more favorable in the centre of species' ranges (e.g. Hengeveld and Haeck 1982, Brown 1984, Lawton 1993). Some studies have found lower abundances in central than in peripheral populations (e.g., Carey et al. 1995, Curnutt et al. 1996, Jump and Woodward 2003), but the opposite pattern has been also reported (Ribeiro and Fernandes 2000, Herlihy and Eckert 2005, Kluth and Bruelheide 2005a). Overall, the abundant-centre model has received weak support from recent reviews as a general theory (Sagarin and Gaines 2002, Gaston 2003, Sagarin and Gaines 2006), and more information has to be gathered before general patterns can be determined.

The abundant-centre model has inspired many hypotheses regarding genetic and demographic patterns. For example, the central-marginal model predicts decreasing genetic diversity towards the periphery of species' ranges, due to processes such as genetic drift, inbreeding or reduced gene flow (Brussard 1984). There is evidence for (e.g., Cwynar and MacDonald 1987, Kuittinen et al. 1997, Lammi et al. 1999) and against (e.g., Tigerstedt 1973, Hamrick et al. 1989, Yakimowski and Eckert 2008) this theory, although the pattern of lower genetic diversity in range edges is supported in the majority of cases (Eckert et al. 2008). From a demographic perspective, peripheral populations have often been assumed to show lower values in vital rates, higher temporal fluctuations or higher vulnerability to stochastic events (Lawton 1993, Lesica and Allendorf 1995, Vucetich and Waite 2003). However, while some studies have found lower survival (Carey et al. 1995), seed production (García et al. 2000, Jump and Woodward 2003), or seedling recruitment (Tremblay et al. 2002) in peripheral populations, others have reported increased values in vital rates towards range edges (e.g. Kluth and Bruelheide 2005b, Angert 2009, Samis and Eckert 2009). In this context, the distinction between geographical and ecological marginality might be crucial (Soulé 1973). Indeed, geographically peripheral populations may be found in ecologically favorable conditions (Lennon et al. 2002), whereas populations far from the periphery may occur in ecologically marginal environments or atypical habitats (Grant and Antonovics 1978, Shumaker and Babble 1980). Given that widespread plants frequently encounter different biotic and abiotic conditions throughout their distribution, comparative studies should both consider the location of populations within species' ranges and analyze variation in the most relevant environmental parameters.

2.3. Natural selection vs. neutral demographic processes

Large-scale studies also allow us to analyze evolutionary and historical processes in plants. Phenotypic variation in ecologically relevant traits is expected to be shaped by selective agents, such as climate or other relevant environmental factors, as seen above. In contrast, genetic diversity is typically measured in neutral loci (Lynch et al. 1999, Holderegger et al. 2006), and may instead reflect the consequences of random demographic processes experienced by populations in the past (Holderegger et al. 2006, Mitchell-Olds and Schmitt 2006, Lawton-Rauh 2008). This is frequently encountered along the central-peripheral gradient, in which gene flow tends to decrease towards range edges, favoring isolation and increasing the influence of genetic drift and founder effects in peripheral populations (Lesica and Allendorf 1995, Vucetich and Waite 2003). Thus, analyzing the effects of natural selection and range position on the phenotypic and genetic variation of populations might also help to understand the causes of variability in life-history traits.

3. Study species

The genus *Plantago* contains several herbaceous taxa with a nearly cosmopolitan distribution, such as *P. lanceolata*, *P. major* or *P. media*, characterized many times by a notable ecological, life-history and genetic variation (Kuiper and Bos 1992). For the present work, we have chosen a widespread and particularly variable short-lived herb, *Plantago coronopus* L. We have restricted our study to *P. coronopus* ssp. *coronopus*, which is the most common subspecies throughout the range and differs from the others in the morphology of the bracts (Chater and Cartier 1976, Pedrol 2009). Still, this is a very complex and polymorphic taxon, and future taxonomic reorganizations within the species should not be discouraged (J. Pedrol, *personal communication*). For simplicity, we will hereafter refer to the studied subspecies as *P. coronopus*.

The distribution of *P. coronopus* ranges from North Africa to North Europe, and the species also extends to SW Asia (Hultén and Fries 1986). In North Europe, the species is frequently restricted to coastal areas, although it seems to be expanding inland (and to coastal areas of other continents; Global Biodiversity Information Facility, http://www.gbif.org). *P. coronopus* can be found in different habitats, such as sand dunes, coastal prairies or human-modified areas, which are usually characterized by relatively low levels of competition from other plants, or by disturbances such as human and cattle trampling (Dodds 1953, Chater and Cartier 1976, Pedrol 2009).

In addition to its wide distribution and habitat diversity, *Plantago coronopus* shows a large variability in several ecological and life-history traits. For example, it presents either annual or short-lived perennial populations (Chater and Cartier 1976), though no corresponding variation has been found in life-history components such as fruit set, seed production or seed mass (Braza et al. 2010). Additionally, plants present flat or ascending rosettes with numerous leaves, which are very variable in size, pubescence, dentation or degree of succulence. Another sign of the high versatility of *P. coronopus* is its reproductive system. The species is gynodioecious (Koelewijn 1996), with female percentages ranging from *ca*. 10 % to 50% (M. B. García, *unpublished data*). Reproductive individuals produce several spikes with tetramerous flowers that are wind-pollinated (Dodds 1953), and present intermediate to high outcrossing rates, with large variation among populations (ranging from 0.34 to 0.93; Wolff et al. 1988). Interestingly, *P. coronopus* presents seed dimorphism: each fruit may produce up to four big basal seeds, and one or no small apical seed (Dowling 1933). Basal seeds produce a coat that become mucilaginous when moistened, thanks to the presence of pectinic material in the epidermal cells (Gutterman and ShemTov 1996), virtually absent in apical seeds. Mucilaginous coats are thought to affect important processes such as water absorption, competition via allelopathy, adherence to the soil, or DNA protection from irradiation damage (Harper and Benton 1966, Hasegawa et al. 1992, Lu et al. 2010, Yang et al. 2011). Overall, basal seeds show higher germination rates than apical ones (Schat 1981, Braza and García 2011).

Numerous studies have analyzed intrinsic and extrinsic factors affecting the performance of *P. coronopus*. For example, seed production increases with plant size (Braza et al. 2010), and plant density negatively affects vegetative and reproductive performance (Waite and Hutchings 1982, Waite 1984, Hutchings and Waite 1985, Koelewijn 2004a), although the effect of seed density on germination seems to differ between greenhouse and field experiments (Waite and Hutchings 1978, 1979, Schat 1981). In addition, seed size positively affects plant performance, since a larger size in basal seeds leads to an advantage through the plant’s life in terms of germination, size, survival and fecundity (Koelewijn 2004b, Koelewijn and Van Damme 2005). Finally, negative effects from drought, nutrient shortage or salinity stress have been reported on germination, seedling recruitment, and reproductive output (Dowling 1933, Onyekwelu 1972, Waite and Hutchings 1978, Schat 1981, Waite 1984, Schat and Scholten 1985, Woodell 1985, Luciani et al. 2001, Friesberg et al. *in press*).

4. Introduction to the study area and data collection

Many of the above mentioned studies on *P. coronopus* have been carried out in the laboratory (e.g., Waite and Hutchings 1978, Schat 1981, Smekens and van Tienderen 2001, Koelewijn 2004b, Koelewijn and Van Damme 2005), and those in the field spanned small areas of the species' distribution (Onyekwelu 1972, Waite and Hutchings 1979, 1982, Braza et al. 2010, Braza and García 2011). However, to understand the biology of widespread taxa in a comprehensive way, we need to analyze individual and population performance throughout species' ranges, at large spatio-temporal scales.

In the present study, we examine life-history, demographic and genetic variation in up to 22 populations of *P. coronopus* in Europe and North Africa, spanning most of the species latitudinal gradient (Fig. 1; Table 1; Appendix 1, 2, 3 and 4). We selected only perennial populations (which are more common across the species' latitudinal range) to reduce the variables affecting our comparative analysis, as our focus was on the effects of geographical and environmental gradients. For our purposes, we carried out intensive monitoring in the period 2007-2010 (Appendix 5) in four central populations in Spain (T, CA, C and TB) and six northern peripheral populations in Denmark (DH and DS), Sweden (SG and ST) and Scotland (EA and ES). In these populations, we collected field data (life-history and

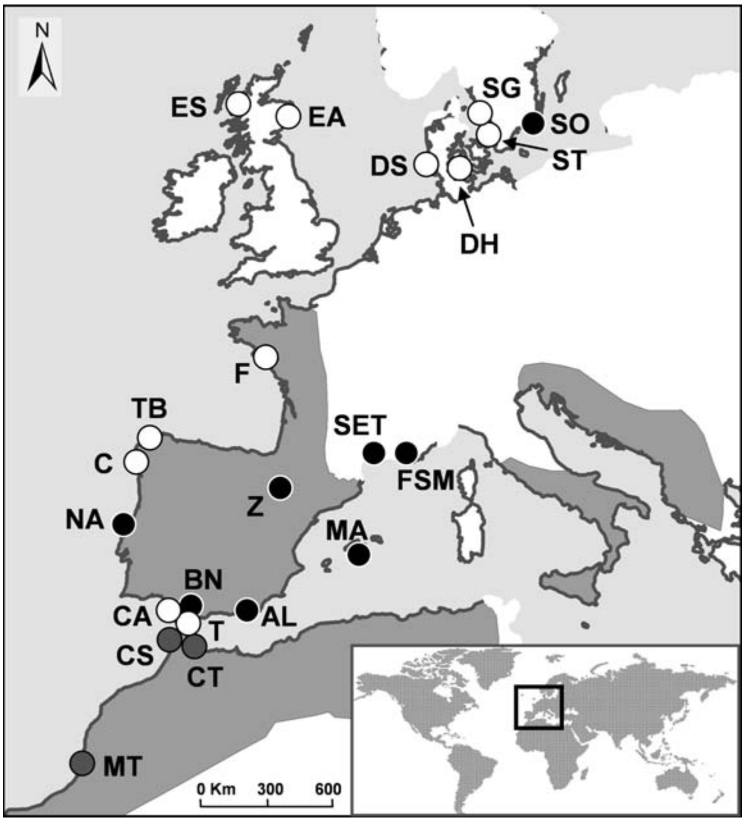

Fig. 1 Distribution map with sampled populations of *Plantago coronopus* in Chapters 1 and 2 (demographic analyses; white dots), Chapter 3 (analysis of variation in reproductive traits among populations; white and grey dots), and Chapter 4 (analyses of phenotypic and genetic variation within populations; white and black dots except for TB). In grey, distribution range of *Plantago coronopus* (including coastal outlines in dark grey) according to Hultén and Fries 1986).

demographic traits) and plant material (seeds and leaves for analyses of reproductive traits and genetic diversity, respectively) that constituted the main source of information for the present study. We also used field data previously gathered from two additional populations of *P. coronopus* located in France (F) and Spain (BN), and from one extra year for a subset of the monitored populations (T, C, F, DS, SG and ST; R. Braza and M. B. García). To increase sample size in the analyses of seed traits and genetic diversity, we also obtained plant material from three and eight additional populations, respectively (Fig. 1, Table 1).

Table 1 Populations of *Plantago coronopus* sampled in this study. Information is given about their location, geographical coordinates, habitat and chapters of this thesis where each population is analyzed.

Population	Location	Coordinates	Habitat	Chapters
MT	Tiznit (Morocco)	29º45’ N, 09º53’ W	Coastal cliff	3
CS	Cap Spartel (Morocco)	35º47’ N, 05º55’ W	Coastal cliff	3
CT	Ceuta (Spain)	35º54’ N, 05º21’ W	Coastal cliff	3
T	Tarifa (Spain)	36º02’ N, 05º38W	Sand dune	1, 2, 3 & 4
CA	Camposoto (Spain)	36º25’ N, 06º13W	Sand dune	1, 2, 3 & 4
BN	Bosque Niebla (Spain)	36º06’ N, 05º32’ W	Forest gaps	1, 2, 3 & 4
AL	Almería (Spain)	36º43’ N, 02º11’ W	Sandy cliff	4
NA	Nazare (Portugal)	39º35’ N, 09º04’ W	Sand dune	4
MA	Mallorca (Spain)	39º46’ N, 03º45’ E	Sand dune	4
Z	Zaragoza (Spain)	41º39’ N, 0º50’ W	Riverside	4
C	Corrubedo (Spain)	42º33’ N, 09º01’ W	Sand dune	1, 2, 3 & 4
TB	Traba (Spain)	43º11’ N, 09º03’ W	Sand dune	1, 2 & 3
SET	Sète (France)	43º24’ N, 03º39’ E	Lagoon rocks	4
FSM	Fos sur mer (France)	43º27’ N, 04º52’ E	Lagoon rocks	4
F	Bretagne (France)	47º18’ N, 02º30’ W	Sand dune	1, 2, 3 & 4
DH	Helnaes (Denmark)	55º08’ N, 09º59’ E	Coastal meadow	1, 2, 3 & 4
DS	Skallingen (Denmark)	55º29’ N, 08º15’ E	Coastal meadow	1, 2, 3 & 4
SO	Ottenby (Sweden)	56º13’ N, 16º24’ E	Coastal meadow	4
ST	Torekov (Sweden)	56º23’ N, 12º38’ E	Coastal meadow	1, 2, 3 & 4
SG	Glommen (Sweden)	56º55’ N, 12º21’ E	Coastal meadow	1, 2, 3 & 4
EA	Aberdeen (Scotland)	57º20’ N, 01º55’ W	Coastal meadow	1, 2, 3 & 4
ES	Skye (Scotland)	57º30’ N 06º26’ W	Coastal meadow	1, 2, 3 & 4

Objectives

Objectives

The general objective of this thesis is to analyze the variability in population dynamics, life-history traits, and genetic diversity across the latitudinal range of the short-lived herb *P. coronopus*, in relation with 1) the position of populations within the species' range and 2) the most relevant environmental gradients at different spatial scales. In this way, we aim to better understand the causes underlying the success of widespread plants over large distribution areas, and how such variability is structured in time and space. The specific objectives associated to the different chapters of the study are the following:

Chapter 1

In the first chapter, we test the predictions from classical central-marginal theories in *P. coronopus*, by comparing density and mean values and variability in vital rates between central and northern peripheral populations in Europe. We also analyze the effects of environmental factors on vital rates, and evaluate the ecological marginality of populations across the species' range.

Chapter 2

In the second chapter, we combine the different vital rates of the life cycle to calculate stochastic population growth rates, in order to compare overall population performance between central and peripheral regions. We also evaluate the contribution of each life cycle component to differences in population growth rates at two spatial scales, between and within regions. Finally, we analyze the relationship between variation in population dynamics and variation in environmental conditions.

Chapter 3

We analyze in detail several reproductive traits and their variability among populations, in a large latitudinal gradient from North Africa to North Europe. We search for relationships between these traits and environmental conditions, and analyze the possible trade-offs involved in resource allocation to seeds at the fruit and individual level. In particular, we test whether a trade-off between fecundity and stress tolerance of seeds promotes variability among populations in reproductive traits such as seed size and proportion of two seed morphs.

Chapter 4

We explore the patterns and causes of phenotypic and genetic variation in a large number of populations across Europe. In particular, we aim to disentangle the effects of environmental selective agents from the influence of range position, in order to better understand the historical and evolutionary processes that might have shaped variation within populations of *P. coronopus*.

Publications

Chapter 1

Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus*

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Peripheral populations have long been predicted to show lower vital rates, higher demographic fluctuations, and lower densities than central populations. However, recent research has questioned the existence of clear patterns across species' ranges. To test these hypotheses, we monitored five central and six northern peripheral populations of the widespread herb *Plantago coronopus* along the European Atlantic coast during 5 yr. We estimated population density, and calculated mean values and temporal variability of four vital rates (survival, individual growth, fecundity and recruitment) in hundreds of plants in permanent plots. Central populations showed higher fecundity, whereas peripheral populations had higher recruitment per reproductive plant, indicating a higher overall reproductive success in the periphery. Central populations showed a marginally significant tendency for higher growth, and there were no differences between range positions in survival. Fecundity and growth were affected by intraspecific competition, and recruitment was affected by precipitation, highlighting the importance of local environmental conditions for population performance. Central and peripheral populations showed no significant differences in temporal variability of vital rates. Finally, density was significantly higher in peripheral than in central populations, in discrepancy with the abundant-centre model. Density was correlated to seedling recruitment, which would counterbalance in peripheral populations the lower fecundity and the tendency for lower growth of established plants. Such compensations among vital rates might be particularly common in widespread plants, and advise against simplistic assumptions of population performance across ranges. The whole species' life cycle should be considered, since different arrangements of vital rates are expected to maximize fitness in local environments. Our results show also the importance of discerning between geographical periphery and ecological marginality. In a context of climate-induced range shifts, these considerations are crucial for the reliability of niche-models and the management of plant peripheral populations.

Peripheral populations are a popular topic of research in ecology, evolutionary biology and genetics (Eckert et al. 2008, Sexton et al. 2009). These studies provide insight into critical phenomena such as speciation, adaptive radiation, and natural selection (Grant and Antonovics 1978, Holt and Keitt 2005), and there is a strong debate about their evolutionary potential (Lesica and Allendorf 1995), particularly in the context of global warming and its effects on range-margin dynamics (Hampe and Petit 2005). For example, northern populations often constitute leading edges in species' distribution shifts in the northern hemisphere (Travis and Dytham 2004). Additionally, it is important to evaluate intraspecific variation in population performance across ranges, to improve the reliability of comparative analyses across taxa (Frederiksen et al. 2005) and of niche-based models forecasting biodiversity responses in future ecological scenarios (Lavergne et al. 2010).

The abundant-centre model predicts higher densities in central than in peripheral populations due to more favourable conditions in the core of species' ranges (Hengeveld and Haeck 1982, Brown 1984). This model has been a tenet in much theoretical and empirical research, e.g. in the central-marginal model, which predicts decreasing genetic diversity towards the range periphery (Brussard 1984). In a demographic context, lower density, greater isolation and lower habitat suitability at the periphery are often referred as the main causes to expect lower values in vital rates, higher variability in abundance or higher vulnerability to stochastic events (Lawton 1993, Lesica and Allendorf 1995, Vucetich and Waite 2003). However, although some studies have reported an actual decrease in abundance towards range margins (Carey et al. 1995, Curnutt et al. 1996, Jump and Woodward 2003), the abundant-centre theory has received weak support in recent reviews (Sagarin and Gaines 2002, Gaston 2003, Sagarin et al. 2006), which inevitably questions some of the above predictions based on the model (Eckert et al. 2008).

Demographic performance of populations seems to be indeed rather variable across many species' ranges (Carey et al. 1995, Nantel and Gagnon 1999, García et al. 2000, Kluth and Bruelheide 2005a, Purves 2009), probably reflecting specific local environmental conditions. In addition, populations at the range margin may or may not be considered marginal from an ecological point of view (Grant and Antonovics 1978, Herrera and Bazaga 2008). Although both concepts often overlap, not all ecologically marginal populations are peripherally located, and not all geographically peripheral populations are ecologically marginal (Soulé 1973). Peripheral populations may occur in locally favourable conditions (Lennon et al. 2002), such as high water availability, high soil organic matter content or low competition. Thus, there is no reason to expect that individuals in peripheral populations will always under-perform relative to those in central populations. While some studies have found lower fecundity (García et al. 2000, Jump and Woodward 2003), recruitment (Tremblay et al. 2002) or survival (Carey et al. 1995) in peripheral populations, others have reported increased values in different vital rates towards range edges (Kluth and Bruelheide 2005a, Angert 2009, Samis and Eckert 2009). Moreover, many widespread plants are exposed to different environments across their distribution, yet appear to be well adapted to these varied conditions (Joshi et al. 2001). In these cases, different fitness components such as survival, growth, fecundity or recruitment may show different patterns across the range. For example, Doak and Morris (2010) illustrated how life histories of two tundra plants change in the southern limit, where higher individual growth counteracts lower survival and recruitment rates, and Suryan et al. (2009) reported intraspecific trade-offs between survival and fecundity in marine taxa present both in the Atlantic and the Pacific Ocean. Thus, a correct assessment of population performance across species' distributions should analyze the full spectrum of vital rates and consider variation in local environmental conditions.

Variability in vital rates may also be very important when analyzing demography across species' ranges (Gould and Nichols 1998, Morris and Doak 2004), as it usually reduces long-term population growth (Gillespie 1977). Populations seem to fluctuate more in peripheral than in central areas (Gaston 2009, Sexton et al. 2009), although most research on this topic has been done with animals (Curnutt et al. 1996, Williams et al. 2003). In plants, few range-wide studies have specifically analyzed temporal variation of vital rates. Some of them confirmed the expected higher variability in peripheral areas (Nantel and Gagnon 1999, Gerst et al. 2011), but others did not (Volis et al. 2004, Kluth and Bruelheide 2005a, Angert 2009). However, many of these studies lasted no more than 3 yr, analyzed few populations per species and did not consider the effects of sampling error, which can artificially increase the real variability found in nature (Gould and Nichols 1998). Thus, multi-population approaches with accurate measurements of the variation in vital rates are needed to reach general conclusions about plant dynamics across ranges.

Recent reviews of population performance in central and peripheral areas of species' distributions (Gaston 2009, Sexton et al. 2009) show that generalizations are difficult to establish, partly because few studies are designed to cover a significant fraction of species spatio-temporal variability. In the present work we analyze variation in vital rates and density in the widespread *Plantago coronopus* subsp. *coronopus*, a circum-Mediterranean short-lived herb also present in the coasts of northern Europe. We collected demographic data over 5 yr from ca 11 000 individuals in five central and six northern peripheral populations along the European Atlantic coast. Using this spatially and temporally extensive dataset, we tested the following hypotheses: 1) peripheral populations show lower average vital rates, i.e. survival, individual growth, fecundity and recruitment, than central populations; 2) peripheral populations exhibit higher temporal variability in vital rates; and 3) peripheral populations show lower density. We also analyze the effects of intraspecific competition, precipitation and soil richness, to account for differences in vital rates across the species' range, and we discuss our results in the context of geographical periphery vs ecological marginality.

Material and methods

Species and populations studied

Plantago coronopus (Plantaginaceae) is a widespread, short-lived herb that occurs from north Africa and the Iberian Peninsula to SE Asia. It reaches north Europe through a narrow strip along the Atlantic coast (Hultén and Fries 1986; Fig. 1). We have focussed on the subspecies *coronopus*, which is present throughout the whole species' distribution and differs from other much less widespread subspecies in the morphology of the bracts (Chater and Cartier 1976). Hereafter, we will refer to it as *P. coronopus*. Individuals have one or a few basal rosettes, and produce several spikes with wind-pollinated flowers. Spontaneous autogamy is possible but very variable among and within populations, and fruit set is very high (between 80 and 100%; Villellas et al. unpubl.).

Plantago coronopus is present in a wide variety of environmental conditions across its range, in terms of climate, soil richness and vegetation cover. In central areas, the species is found in coastal and inland locations, in contrasting habitats such as sand dunes, shrublands or human-disturbed areas, and as annual or short-lived perennial life-forms (Chater and Cartier 1976). In contrast, northern populations are restricted to coastal areas, such as seashore meadows or salt marshes, and present a short-lived perennial life-form. For our study, we chose 11 perennial populations along the Atlantic coast (Fig. 1, Table 1) to minimize habitat differences across the species' distribution. We spanned more than two thirds of the whole subspecies latitudinal range (Hultén and Fries 1986), encompassing a substantial part of its ecological variation in coastal environments. We monitored five central populations in sand dunes of S and NW Spain, and NW France, along a latitudinal transect of ca 1500 km; we also monitored six peripheral populations in coastal meadows of S Denmark, SW Sweden and N Scotland, along a longitudinal transect of ca 1500 km. All populations contained thousands of individuals.

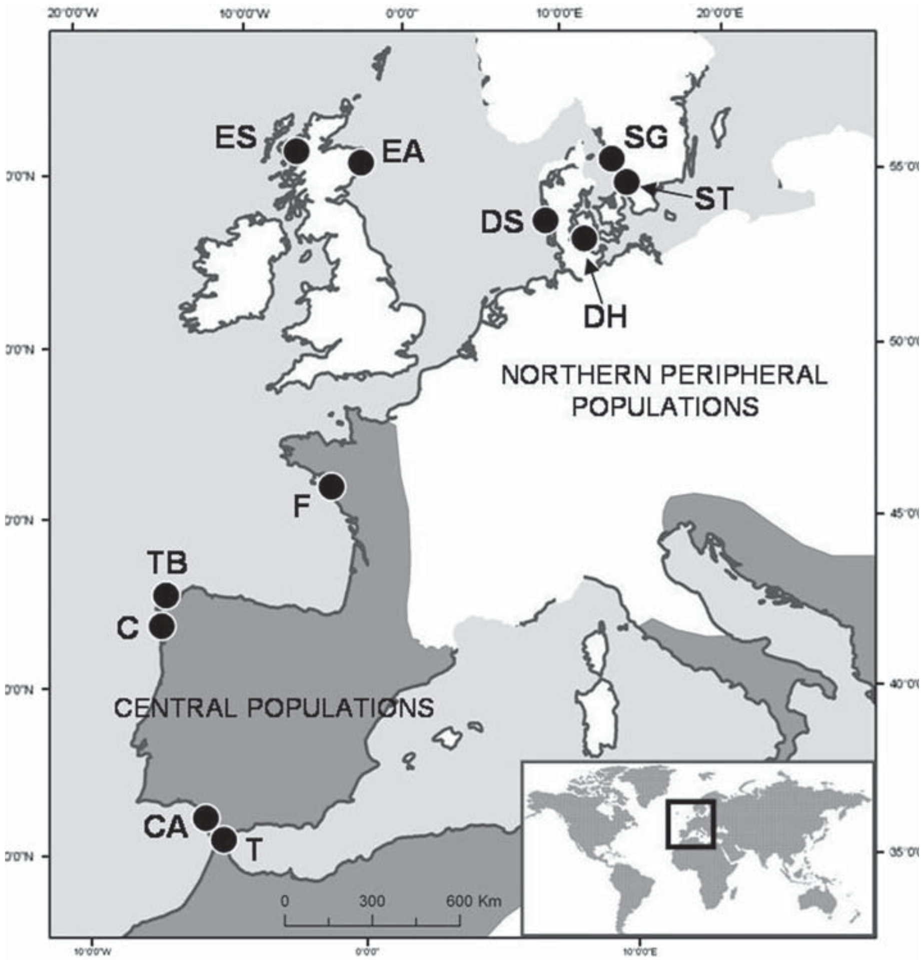

Figure 1. Location of central and peripheral populations of *Plantago coronopus* in this study (black dots). The distribution range of the species and the subspecies *coronopus* is highlighted in grey (including the coastal outlines) according to Hultén and Fries (1986). Notice the species is restricted to coastal locations in the northern periphery. See Table 1 for population acronyms.

Monitoring and data collection

Field data were collected in the period 2007–2010, except for the population F, which was monitored in the period 2003–2006. However, we verified that the average and the variance of climatic variables at site F were similar between both sampling periods. To calculate vital rates, we monitored all the populations over 4 yr, yielding three annual transitions. An additional fifth year of data was collected in a subset of three central and three peripheral populations (2006 for T, C, DS, SG and ST, and 2007 for F), and used for the analysis of temporal variability in vital rates (Table 1; see below). In the first year of study for each population, we established randomly-distributed permanent plots that

Table 1. Characterization of central and peripheral populations of *Plantago coronopus* in the study area. See methods for details on the estimation of plant size (cm), population density ± SE (ind m^{-2}), percentage vegetation cover (by other plant species), SOM (percentage of soil organic matter content), mean annual precipitation (mm) and its coefficient of variation (CV).

Position	Population	Location	Years of study	Plant size	Population density	Vegetation cover (%)	SOM (%)	Precipitation (and CV)
Central	Tarifa (T)	36°02′N, 5°38′W	5	91.3	10.3 ± 2.9	0–25	0.7	634 (0.18)
	Camposoto (CA)	36°25′N, 6°13′W	4	152.4	13.2 ± 2.8	0–25	0.4	608 (0.25)
	Corrubedo (C)	42°33′N, 9°01′W	5	36.0	212.1 ± 43.5	0–25	1.1	1003 (0.29)
	Traba (TB)	43°11′N, 9°03′W	4	28.2	145.8 ± 39.1	25–50	1.4	842 (0.20)
	Pen Bron (F)	47°18′N, 2°30′W	5	56.2	182.6 ± 112.6	25–50	0.9	680 (0.37)
Peripheral	Helnaes (DH)	55°8′N, 9°59′E	4	62.9	112.4 ± 20.6	75–100	5.6	757 (0.17)
	Skallingen (DS)	55°29′N, 8°15′E	5	48.9	175.8 ± 71.0	75–100	17.9	906 (0.17)
	Glommen (SG)	56°55′N, 12°21′E	5	25.1	579.5 ± 173.1	75–100	0.8	962 (0.24)
	Torekov (ST)	56°23′N, 12°38′E	5	41.9	268.3 ± 63.7	75–100	6.1	733 (0.21)
	Aberdeen (EA)	57°20′N, 1°55′W	4	40.8	388.4 ± 19.1	75–100	18.1	840 (0.13)
	Skye (ES)	57°30′N, 6°26′W	4	27.1	498.5 ± 17.9	75–100	17.7	2020 (0.16)

varied in number (3 to 10) and size (0.25 to 5 m^2) depending on local plant density. Annual censuses were done during fruit maturation and before seed dispersal. Due to regional differences in phenology, central populations were monitored in July and peripheral populations in August. In each census, we recorded between 100 and 400 individuals older than 1-yr within the plots, which we relocated the following year with the aid of tags and hand-drawn maps showing the position of plants. For each individual, we recorded life stage as vegetative (V) or reproductive (R), the number of leaves and inflorescences, and the length of an average leaf and an average inflorescence. We also counted and mapped new seedlings in each census.

Growth, fecundity and survival rates of *P. coronopus* were then calculated annually for all non-seedling individuals monitored in the plots. We estimated plant growth rate as the ratio between plant size in a given year and that in the previous year. Plant size was defined as number of leaves × length of an average leaf. We estimated fecundity in reproductive individuals as number of inflorescences × length of an average inflorescence × number of seeds per unit of inflorescence length (calculated with a regression equation for each population). We also calculated the total number of reproductive years and the lifetime fecundity (total seed production over the lifespan) of those reproductive individuals that were monitored for their entire lives. Recruitment was estimated within each plot as the number of new seedlings in a given year divided by the number of reproductive individuals present in the previous year (the seed bank contribution is negligible in this species).

Plant density (D) was estimated annually from linear transects (Strong 1966) using the equation $D = \Sigma(1/d) \times (1/T)$, where T is total transect length (it varied from 10 to 200 m depending on local density), and d is the diameter perpendicular to the transect of non-seedling plants intercepting the transect.

Environmental factors were estimated as follows. In all populations, we collected 10 cm deep soil cores the first year, to estimate soil organic matter content from the organic carbon (Heanes 1984). We obtained annual precipitation data for the sampling period from public databases: Spanish National Meteorological Agency (T and CA); MeteoGalicia (C and TB); MeteoFrance (F); Danish Meteorological Inst. (DH and DS); Swedish Meteorological and Hydrological Inst. (SG and ST); and Met Office (EA and ES). For each population, we also calculated the mean annual precipitation and the coefficient of variation (CV) for the sampling period. Intraspecific competition was estimated the first year scanning the maps with the position of each plant within plots, and measuring Voronoi polygons with Arc-GIS (ver. 9.3). These polygons contain the area closer to each plant than to any other conspecific, and thus represent individual resource availability (thereafter 'resource area'). Resource area mainly allowed us to analyze the effects of intraspecific competition on per capita vital rates but, averaged across individuals, constituted an additional estimate of population density. We also measured the abundance of other plant species as percentage of vegetation cover in plots, by using the categories 0–25, 25–50, 50–75 and 75–100%.

Statistical analyses

Statistical analyses were made with SPSS (ver. 17.0) unless specified otherwise. To test for differences in mean vital rates between central and peripheral populations, we used linear mixed models (LMM) for continuous variables, i.e. growth, fecundity and recruitment (log-transformed), and a generalized linear mixed model (GLMM; GLIMMIX procedure, SAS ver. 9.1) for the binomial variable, i.e. survival (Table 2). The central or peripheral position of populations was a fixed factor, and year and population (nested within position) were random factors. The factor plot was not included in the models because according to preliminary analyses it did not affect the significance of position and population. Likewise, interactions between position and year were removed from the analyses when their effect was not significant. Life stage and plant size (log-transformed) were also included in models as a fixed factor and a covariate, respectively. The significance of random factors in the GLMM was evaluated by testing whether z-values (the covariance parameter estimates divided by the standard errors) significantly differed from zero (Juenger and Bergelson 2000). Additionally, we tested for differences between range positions in lifetime fecundity and in mean plant size with LMMs, including plant stage as a fixed factor and year as a random factor in the analysis of plant size.

To analyze the role of environmental factors in the differences in vital rates between range positions (Results), we

Table 2. Comparison of mean vital rates between central and peripheral populations of *Plantago coronopus*. Results from analyses (linear mixed models for fecundity, recruitment and growth, and generalized linear mixed model for survival) and average values per position (± SE).

	Fecundity		Recruitment		Growth		Survival	
	F	p	F	p	F	p	F	p
Effects in analyses								
Position	$13.60_{1,7}$	0.007	$5.07_{1,9}$	0.050	$4.51_{1,11}$	0.057	$1.51_{1,9}$	0.250
Population	39.60_{9}	< 0.001	4.69_{9}	< 0.001	21.21_{9}	< 0.001	0.64 ± 0.31*	0.038
Year	1.83_{2}	0.353	7.86_{2}	0.001	8.82_{2}	0.101	0.44 ± 0.44*	0.308
Position × year	38.29_{2}	< 0.001			4.97_{2}	0.007		
Plant size	1685.97_{1}	< 0.001					156.73_{1}	< 0.001
Life stage					$388.17_{1,4899}$	< 0.001	$49.45_{1,10379}$	< 0.001
Average values								
Central	1089.5 ± 200.0		2.4 ± 0.7		1.7 ± 0.1		42.7 ± 5.1	
Peripheral	203.1 ± 33.0		6.6 ± 1.8		1.3 ± 0.1		53.7 ± 5.7	

*Values correspond to covariance parameter estimates ± SE, instead of F statistic.

tested with a set independent analyses (LMMs) the effect of resource area (as an estimate of intraspecific competition), annual precipitation and soil organic matter on vital rates, and if the effect of position remained significant after controlling for those explanatory variables. First, we analyzed the effect of resource area, including population as a random factor and plant size as a covariate, because of its potential influence on resource area. Second, we tested the effect of annual precipitation, using annual population averages of vital rates and including year as a random factor. Third, the effect of soil organic matter was tested on average population vital rates across all years (here we used a linear model instead of a LMM). In addition, we tested for differences in resource area and in annual precipitation between central and peripheral positions with LMMs (including population as a random factor), and for differences in soil organic matter and in CV in precipitation with t tests.

Temporal variability in vital rates was analyzed in a subset of three central (T, C, F) and three peripheral (DS, SG, ST) populations monitored during 5 yr (four transitions). To accurately estimate this variability, we firstly accounted for sampling error: for each vital rate, we fitted a model with an intercept and a random factor of year, and we obtained the corrected annual population averages from the coefficients of the random factor (Altwegg et al. 2007, Morris et al. 2011). The analyses applied for such corrections were LMMs for fecundity, growth and recruitment and a GLMM for survival (lme and lmer procedures, respectively, R Development Core Team 2010). Variability in vital rates was then estimated from the CV of the corrected annual values. Survival has a binomial distribution with an inherent limit in variance, so we estimated its relative CV instead: CV/CV_{max}. We calculated CV_{max} from the square root of the ratio between $(1-p)$ and p, where p is mean survival rate (Morris and Doak 2004). For each vital rate we tested for differences between central and peripheral populations in variability (CV) with t tests. We also analyzed overall differences in variability between range positions considering all vital rates together (except for survival), by performing a LMM with position as a fixed factor and vital rate as a random factor.

We finally compared density between central and peripheral populations with a LMM. The position of populations was included as a fixed factor and population as a random factor. We also tested with a linear model whether density was correlated to recruitment, using average population values across years, and including position as a fixed factor.

Results

Mean vital rates in central and peripheral populations

Plants had significantly higher fecundity in central than in peripheral populations of *P. coronopus* (Table 2, Fig. 2). There were no differences between range positions, however, in the average number of reproductive years per individual: between 1.12 (population F) and 1.40 (T) in central populations, and between 1.14 (DH) and 1.44 (ST) in peripheral ones. The analysis of lifetime fecundity confirmed a higher total seed production in central areas ($F_{1,2617} = 35.67$,

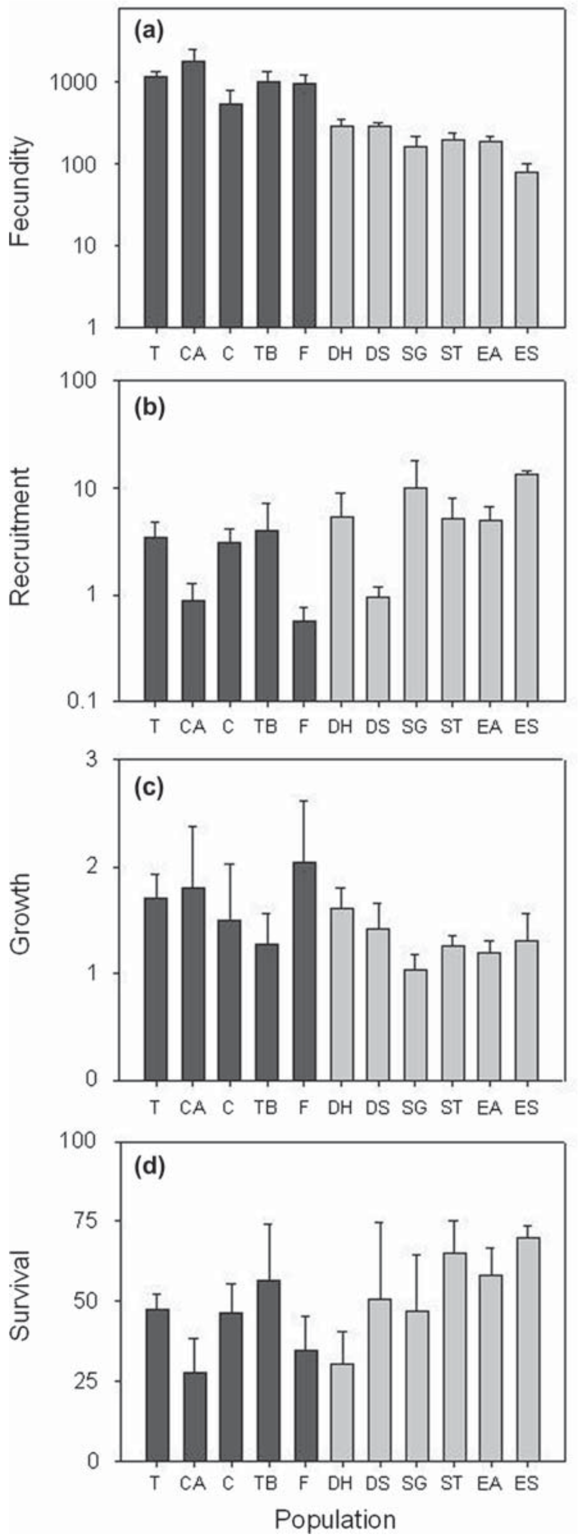

Figure 2. Annual averages of vital rates in central (dark bars) and peripheral (light bars) populations of *Plantago coronopus* (± SE). Vital rates are (a) fecundity, measured as number of seeds per year and reproductive plant; (b) recruitment, measured as number of seedlings in a given year divided by number of reproductive plants in the previous year; (c) plant growth, measured as size in a given year divided by size in the previous year; and (d) survival, measured as percentage of surviving individuals. Notice the logarithmic scale of the vertical axis in (a) and (b).

$p < 0.001$). In contrast with fecundity, peripheral populations showed a significantly higher recruitment than central populations (Table 2, Fig. 2).

Central populations showed a marginally significant tendency for higher plant growth rates than peripheral populations, and there were no significant differences in survival between positions (Table 2, Fig. 2). Populations differed significantly within range positions for all vital rates. Plant size was positively correlated with fecundity and survival (Table 2) but did not differ between central and peripheral populations ($F_{1,9} = 1.05$, $p = 0.331$).

Effects of competition and environmental factors on vital rates

Plants in central populations had a significantly larger resource area ($F_{1,8} = 30.60$, $p < 0.001$) and lower soil organic matter content ($t_9 = -2.89$, $p = 0.018$) than in peripheral populations. Precipitation was lower on average in central locations (754 mm) than in peripheral ones (1036 mm), although not significantly ($F_{1,9} = 1.50$, $p = 0.252$), and variability in precipitation was marginally higher in central populations ($t_9 = 2.21$, $p = 0.055$). In addition, vegetation cover was consistently higher in peripheral populations (Table 1).

Resource area was positively and significantly correlated to growth ($F_1 = 4.81$, $p = 0.030$). Since the effect of position on growth found in previous analyses was not significant after controlling for resource area ($F_1 = 0.08$, $p = 0.784$), this factor explained differences in growth between central and peripheral populations. Resource area was also positively and significantly correlated to fecundity ($F_1 = 68.01$, $p < 0.001$), but the effect of position on fecundity remained significant after controlling for resource area ($F_1 = 12.90$, $p < 0.001$). Precipitation had no significant effect in fecundity ($F_{1,28} = 1.18$, $p = 0.287$) or growth ($F_{1,28} = 0.34$, $p = 0.563$), but did have a significant effect in recruitment ($F_{1,28} = 8.32$, $p = 0.007$). Since the effect of position was not significant after controlling for precipitation ($F_{1,28} = 2.37$, $p = 0.135$), this environmental variable explained differences in recruitment between central and peripheral populations. Finally, soil organic matter had no significant effect in mean values of fecundity ($F_1 = 0.03$, $p = 0.879$), recruitment ($F_1 = 0.17$, $p = 0.691$) or growth ($F_1 = 0.06$, $p = 0.815$). The effect of environmental variables on survival was not analyzed because central and peripheral populations did not differ in this vital rate.

Temporal variability in vital rates

Considering vital rates independently, central populations showed on average higher temporal variability in fecundity and growth, and peripheral populations were more variable on average in recruitment and survival (Fig. 3), but these differences were not significant (fecundity: $t_4 = 0.71$, $p = 0.519$; growth: $t_4 = 0.96$, $p = 0.391$; recruitment: $t_4 = -1.68$, $p = 0.168$; survival: $t_4 = -1.20$, $p = 0.296$). Central and peripheral populations showed no significant differences in overall variability when three of the vital rates (fecundity, growth and recruitment) were analyzed together ($F_{1,2} = 0.28$, $p = 0.647$).

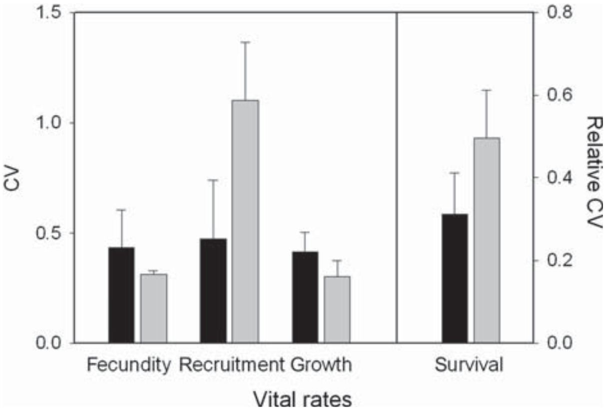

Figure 3. Temporal variability in vital rates in central (dark bars) and peripheral (light bars) populations of *Plantago coronopus*. Variability was calculated from a subset of three central (T, C, F) and three peripheral (DS, SG, ST) populations. Vertical axis represent average values of CV in growth, fecundity and recruitment ± SE (left), and average values of relative CV in survival ± SE (right). See Methods for further details on how relative CV was calculated.

Density in central and peripheral populations

Peripheral populations showed significantly higher densities ($F_{1,9} = 7.73$, $p = 0.021$) than central populations. Density was significantly correlated to recruitment ($F_1 = 7.19$, $p = 0.028$). Since the effect of position was no longer significant after including recruitment in the model ($F_1 = 1.72$, $p = 0.226$), this factor explained differences in density between range positions.

Discussion

Peripheral populations have long been predicted to show lower vital rates, higher demographic fluctuations, and lower densities than central populations (Hengeveld and Haeck 1982, Brown 1984, Lawton 1993, Vucetich and Waite 2003). In our comparative analysis of *P. coronopus*, we found higher fecundity and a tendency for higher growth in central populations. However, northern peripheral populations showed higher recruitment, resulting in higher population density, and exhibited similar temporal variability in vital rates. Thus, our findings diverge from classical predictions, in agreement with other recent studies (Sagarin and Gaines 2002, Angert 2009, Doak and Morris 2010). Differences in demographic performance between central and peripheral populations of this widespread herb seem to be explained by local precipitation and intraspecific competition. We now discuss the main results.

Mean vital rates in central and peripheral populations

Peripheral populations of *P. coronopus* showed a much lower fecundity than central ones. This result agrees with other studies reporting reduced seed production or seed quality at the species' range margin (Pigott and Huntley 1981, García et al. 2000, Jump and Woodward 2003), although the pattern does not seem to be general (Kluth and Bruelheide 2005a, Yakimowski and Eckert 2007). Fecundity was positively correlated with size in *P. coronopus*, a common pattern in plants (Hendriks and Mulder 2008). However, we found no significant differences in plant size between range positions. Fecundity was also negatively affected by intraspecific competition, attending to the significant correlation between seed production and resource area (see also Waite and Hutchings 1982), and this effect might have been further increased in peripheral locations by a higher vegetation cover. Thus, to some extent, competition for resources seems to limit seed production in northern peripheral populations of *P. coronopus*, although only removal experiments would confirm such hypothesis. However, differences in fecundity between central and peripheral populations seem to be also determined by factors not considered in this study, since the effect of position remained significant after controlling for plant size and intraspecific competition.

In contrast to fecundity, recruitment rate was higher in peripheral populations, in agreement with the pattern reported by Samis and Eckert (2009) for another coastal plant (but see Tremblay et al. 2002, Castro et al. 2004). Recruitment was estimated in our study as the presence of new seedlings in a given year relative to the number of reproductive individuals in the previous year. Hence, this measure includes three fitness components, i.e. fecundity, germination and early survival, which estimate overall reproductive success better than seed production alone. It is thus noteworthy that although fecundity was higher in central populations, overall reproductive success was higher in the periphery. Similarly, diverging patterns in seed production and germination rates have been found between central and peripheral populations of other annual and perennial species (Kluth and Bruelheide 2005a, Yakimowski and Eckert 2007). Altogether, these results highlight the necessity to consider different vital rates when analyzing population performance, and particularly warn against assessing reproductive success from fecundity data alone. The lower recruitment in central populations of *P. coronopus* might respond to their occurrence in sand dunes, a harsh habitat with unstable soils where seedling establishment is extremely hazardous (Crawford 2008). In contrast, the higher and less variable precipitation in the coastal meadows of northern locations offers more favourable conditions for recruitment in terms of water availability (Castro et al. 2004).

Survival and growth rates did not differ between central and peripheral populations of *P. coronopus*. However, there was a marginal tendency in central populations to present higher growth, which seems to be correlated to a lower intraspecific competition in their locations. The few studies carried out on survival and individual growth across other plant species' ranges are also inconclusive: some reported reduced survival rates in peripheral populations (Carey et al. 1995), while others did not find a consistent pattern (Angert 2009, Gerst et al. 2011). Regarding growth, Jump et al. (2006) reported lower values in marginal populations in *Fagus sylvatica*, whereas Purves (2009) found diverging results between northern and southern edges in an ample survey of trees in US, although spatial scales were not comparable in both studies.

Our study showed thus important differences in vital rates between central and peripheral populations of *P. coronopus*. However, beyond the central-peripheral comparison, significant differences among populations were also detected within regions for all vital rates (Fig. 2), which highlights the interest of analyzing demographic patterns of widespread species at different geographical scales. Some patterns found in vital rates across the species' range were linked to precipitation or intraspecific competition. Local environmental conditions, therefore, may have a crucial role in population performance, not only when comparing different parts of the distribution area, but also at lower scales. Indeed, large variation in local conditions has been found within central and peripheral regions of *P. coronopus*, e.g. in precipitation regime (Table 1).

Temporal variability in vital rates

Peripheral populations of *P. coronopus* showed a higher average temporal variability in recruitment and survival than central ones, but fecundity and growth were on average more variable in central locations, and more importantly, none of these differences were significant. Although the analyses of single vital rates were not completely reliable due to low sample sizes (six populations), the opposite tendencies in fecundity and growth with respect to recruitment and survival revealed no clear patterns in temporal variability between range positions, in contrast with classical predictions. This was confirmed by the overall analysis of variability, which did not show significant differences between range positions either.

The lack of pattern in *P. coronopus* is not surprising, considering the discrepancy among the few related studies carried out with other plant species. On the one hand, fecundity and survival were more variable in peripheral than in central populations in several annual taxa (Gerst et al. 2011), and higher fluctuations were also reported in mortality for peripheral populations of two perennial species (Nantel and Gagnon 1999). In contrast, survival was more variable in marginal populations in the perennial *Mimulus lewisii* but not in its congener *M. cardinalis* (Angert 2009), fecundity and survival showed higher variability in the range centre of the annual *Hornungia petraea* (Kluth and Bruelheide 2005a), and there were no differences between range positions in variation of population growth rates in the annual *Hordeum spontaneum* (Volis et al. 2004). Thus, besides the relative scarcity of studies, there seems to be a mismatch between classical predictions and the heterogeneous conclusions provided by empirical research, which hinders the establishment of general patterns in plant performance across species' distributions.

Density in central and peripheral populations

Our study of *P. coronopus* does not support the abundant-centre model, as northern peripheral populations showed higher densities than central populations. The higher average values of resource area in central locations indicated a sparser distribution of plants in these populations, and confirmed the differences found in density. The widely accepted idea that species are more abundant in the centre than in the edge of their range has been indeed questioned by recent comprehensive reviews (Sagarin and Gaines 2002, Gaston 2003, Sagarin et al. 2006), and our results confirm that the abundant-centre model can no longer be assumed without previous testing. Differences in vital rates between central and peripheral populations are expected to affect density (Kluth and Bruelheide 2005b), and recruitment seems to be the most determinant factor in the case of *P. coronopus*, attending to its positive relationship with density. The higher establishment of seedlings in peripheral populations, due to higher germination and/or early survival rates, would maintain the higher density of individuals, compensating the lower fecundity and growth in these locations. Our result highlights the importance of the early life stages of plants for population performance in *P. coronopus*, as corresponds for a short-lived species (Silvertown et al. 1996, Picó et al. 2003).

Geographical periphery vs ecological marginality

Peripheral populations are assumed to occur at the extremes of species' niches, where less favourable conditions are expected. *Plantago coronopus* occurs in different habitats in the central part of its range while it is rather restricted to coastal meadows in the northern periphery, indicating that some environmental factors are limiting its spreading northwards. However, the distinction between geographical periphery and ecological marginality is crucial, as these concepts not always overlap in real populations (Soulé 1973, Grant and Antonovics 1978, Herrera and Bazaga 2008). The higher fecundity and growth in central populations of *P. coronopus* suggest more favourable conditions for the development of established plants in dunes, in part due to a positive effect of resource area. This seems to be true for at least three of the five central populations (T, CA, F), which present as well larger plants than most peripheral populations (Table 1). However, northern peripheral locations appear to be more suitable for seedling recruitment, due to higher precipitation. Additionally, northern populations show higher densities of established plants than central populations and similar temporal variability in vital rates, which contrasts with some characteristics ascribed to ecologically marginal populations (Soulé 1973). *Plantago coronopus* is indeed successfully competing with other plant species of similar life histories and resource requirements in the northern coastal meadows, while it behaves as a poor competitor in sand dunes of central areas. Thus, despite a restriction of northern populations of *P. coronopus* to coastal environments, our study shows that habitats may be more favourable at the range periphery, at least for some vital rates (Sexton et al. 2009), and highlights the importance of carefully distinguishing between geographical periphery and ecological marginality when forecasting population performance (but see Gerst et al. 2011).

Final remarks

Theoretical studies often simplify comparisons between central and peripheral populations. However, variation in population performance across species' ranges may be complex, and the best way to understand such intraspecific variation is to carry out large-scale studies of different life cycle components (Sexton et al. 2009, Gerst et al. 2011). The life cycle might actually be regarded as a plastic phenotypic trait (Caswell 1983) that characterizes species in a particular combination of environmental variables, and which may change across ranges. In our study, the contrasting patterns of recruitment, fecundity and growth suggest compensatory changes in vital rates across the range of *P. coronopus*, to adjust the life cycle of populations to their local conditions (Suryan et al. 2009, Doak and Morris 2010). Such variation in the arrangement of vital rates would have allowed this plant to successfully adapt to contrasting environments over large distribution areas.

It is difficult to evaluate to what extent the patterns shown by *P. coronopus* are common among other widespread taxa, but our results contribute to understand that 1) simplistic considerations, such as positive vs negative diagnosis of the status of populations based only on their geographical position, may fail because peripheral populations might not be located in ecologically marginal conditions; 2) assessments of population performance including the full set of vital rates are much more reliable, since low values in some rates can be counterbalanced by high values in others; and 3) the reliability of niche-models predicting future species' distributions under global warming could be greatly improved by considering intraspecific variation in population performance. The management of peripheral populations will significantly gain from studies that show the importance and arrangement of different fitness components in species, and their variability over time and across ranges.

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Chapter 2

Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb

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Analyzing intraspecific variation in population dynamics in relation to environmental factors is crucial to understand the current and future distributions of plant species. Across ranges, peripheral populations are often expected to show lower and more temporally variable vital rates than central populations, although it remains unclear how much any differences in vital rates actually contribute to differences in population growth rates. Moreover, few demographic studies accounting for environmental stochasticity have been carried out both at continental and regional scales. In this study we calculated stochastic growth rates in five central and six northern peripheral populations of the widespread short-lived herb *Plantago coronopus* along the Atlantic Coast in Europe. To evaluate at two spatial scales how mean values and variability of vital rates (*i.e.* fecundity, recruitment, survival, growth and shrinkage) contributed to the differences in stochastic growth rates, we performed Stochastic Life Table Response Experiment analyses between and within central and peripheral regions. Additionally, we searched for correlations between vital rate contributions and local environmental conditions. Lower mean values and greater variability for some vital rates in peripheral than in central populations had an overall negative but non-significant effect on the stochastic growth rates in the periphery. Different life cycle components accounted for differences in population growth depending on spatial scale, although recruitment was the vital rate with the highest influence both between and within regions. Interestingly, the same pattern of differentiation among populations was found within central and peripheral areas: in both regions, one group of populations displayed positive contributions of growth and shrinkage and negative contributions of recruitment and survival, the opposite pattern being found in the remaining populations. These differences among populations within regions in vital rate contributions were correlated with precipitation regime, whereas at the continental scale, differences in contribution patterns were related to temperature. Altogether, our results show how populations of *P. coronopus* exhibit life cycle differences that may enable it to persist in locations with widely varying environmental conditions. This demographic flexibility may help to explain the success of widespread plants across large and heterogeneous ranges.

Key words: Climatic conditions, comparative demography, compensatory shifts in vital rates, core and marginal populations, intraspecific variation, latitudinal gradient, matrix projection models, multiple spatial scales, *Plantago coronopus*, species distribution limits, Stochastic LTRE

Introduction

Peripheral populations have been predicted to show lower densities, lower population growth rates, or higher demographic fluctuations than central populations, due to hypothetically less suitable conditions and higher isolation (Brown 1984, Lawton 1993, Vucetich and Waite 2003). Though some studies found declining performance of plant populations towards range edges (Carey et al. 1995, Nantel and Gagnon 1999, Eckhart et al. 2011), others did not (Angert 2009, Eckstein et al. 2009, García et al. 2010, Doak and Morris 2010), and recent reviews have seriously challenged the validity of these widely accepted predictions (Sagarin and Gaines 2002, Gaston 2009, Sexton et al. 2009). There is actually no reason to expect that population performance will always decrease towards the periphery, as the locations where peripheral populations occur may simply be the ones where the environment is locally favorable for the species, even if such locations are less common near the range limits (Holt and Keitt 2000, Lennon et al. 2002). In addition, while some studies have assessed the means and temporal variability in vital rates and the stochastic population growth rates in central and marginal areas of species' distributions (Angert 2009, Doak and Morris 2010, Eckhart et al. 2011), the relative contributions of differences in vital rate means *vs*. standard deviations to population growth rates across ranges have never been quantified.

Another set of studies has explored spatial variability in population dynamics within limited areas of species' distributions in relation to varying environmental conditions (van Groenendael and Slim 1988, Horvitz and Schemske 1995, Jongejans and de Kroon 2005). However, few studies have examined variability both between and within distinct regions (but see Menges and Dolan 1998, Jongejans et al. 2010), even though the relative importance of different vital rates for population growth may change across spatial scales (Jongejans et al. 2010). Determining which life cycle components have a higher influence on population performance is indeed one of the best ways to analyze intraspecific demographic variation (Morris and Doak 2005). Unraveling the spatial variability of the key processes shaping population dynamics and its possible environmental drivers might help us to discern the causes of range limits (Eckhart et al. 2011), and may enable to project with greater precision the future distributions of species (Keith et al. 2008, Lavergne et al. 2010).

Life Table Response Experiments (LTRE) are very useful in this context because they allow us to evaluate how differences in vital rates contribute to differences in growth rates among populations (Caswell 2001). In addition, this analysis can detect differences in population dynamics even in situations of similar population growth rates, if positive contributions of some life cycle components offset negative contributions of other components. Indeed, compensatory changes in vital rates have been already found among plant populations along environmental gradients (Jongejans and de Kroon 2005, Elderd and Doak 2006, Doak and Morris 2010). Two methodological advances have been incorporated into LTREs in recent studies: the consideration of underlying vital rates, and the use of stochastic rather than deterministic models (Caswell 2010, Davison et al. 2010, Jacquemyn et al. 2012). The former provides more precise assessments of population dynamics because these rates represent distinct biological processes better than projection matrix elements, which may confound several of these processes (Franco and Silvertown 2004). In addition, there is a growing recognition of the potential relevance of environmental stochasticity for the fate of populations (Tuljapurkar et al. 2003; but see Buckley et al. 2010), particularly for short-lived species (García et al. 2008, Morris et al. 2008), as temporal variability generally leads to decreased long-term population growth (Lewontin and Cohen 1969, Gillespie 1977). Stochastic LTREs (SLTRE), thus, constitute a valuable tool to examine the contributions of both the average values and the variation in underlying vital rates to the observed differences in stochastic growth rates (Davison et al. 2010), a considerable advantage with respect to deterministic approaches when analyzing strongly fluctuating vital rates. However, SLTREs have not yet been used to compare stochastic demography between and within central and peripheral areas of species' ranges.

In this study, we analyze intraspecific demographic variation in the widespread short-lived herb *Plantago coronopus*, and apply SLTRE to assess the effects of differences in vital rates between and within distinct regions of its distribution. Previous studies have shown that populations of *P. coronopus* differ substantially in life history and demography, both at local (Waite and Hutchings 1982, Braza et al. 2010, Braza and García 2011) and continental scales (Villellas et al. 2012, Villellas and García 2012). Across the species' latitudinal gradient, for example, central populations showed higher fecundity, whereas northern peripheral populations presented higher recruitment (Villellas et al. 2012). However, no clear pattern emerged between central and peripheral regions in temporal variability of vital rates, and it remains untested whether differences among populations in mean performance and demographic variability result in differences in long-term population growth rates. Even within regions, *P. coronopus* is exposed to a variety of environments, which may trigger demographic variation at different spatial scales. Identifying the environmental factors associated with variation in population dynamics over time and across ranges is indeed crucial for understanding plant demography (Holt and Keitt 2005, Buckley et al. 2010, Eckhart et al. 2011).

Here we present an integrative analysis of population dynamics of the widespread short-lived herb *P. coronopus*, using a 4-yr demographic dataset from five central and six northern peripheral populations. To our knowledge, this is the first study that performs a SLTRE at different spatial scales in a nested fashion (continental and regional), analyzing central and peripheral populations of a plant, and accounting for sampling variation in the estimation of temporal demographic variability. First, we tested whether peripheral populations had lower stochastic growth rates than central populations, and examined how differences in vital rates means and fluctuations between the center and the periphery contributed to differences in stochastic population growth. Second, we tested whether the same vital rates were responsible for demographic variation between and within regions. Third, we analyzed the relationship between variation in population dynamics and variation in environmental conditions, *i.e.*, climate, soil fertility, and intraspecific competition.

Methods

Study species and populations

Plantago coronopus L. (Plantaginaceae) is a common, short-lived herb present from North Africa and the Iberian Peninsula to SW Asia. It also extends to North Europe in a narrow strip along the Atlantic coast and the Baltic Sea, and along the coasts of the United Kingdom (Hultén and Fries 1986). We chose the subspecies *coronopus* (hereafter *P. coronopus*), which is the most common one throughout the species' distribution. Plants have one or a few basal rosettes, and produce spikes with wind-pollinated flowers when they reach reproductive stage (which they sometimes do in their first year).

Plantago coronopus occurs in a variety of environmental conditions, regarding climate, vegetation cover and soil fertility. The species is present both in coastal and inland locations in the range center, where it may grow in dunes, shrublands or human-disturbed areas, and where populations present either annual or short-lived perennial life-forms (Chater and Cartier 1976). Northern populations are rather restricted to the coast, in seashore meadows and salt marshes, presenting a short-lived perennial life-form. For this work we selected 11 perennial populations along the Atlantic coast to minimize habitat differences, as our focus was on the latitudinal range rather than the coastal-to-inland axis. We monitored five central populations in sand dunes in Spain and France, and six northern peripheral populations in coastal meadows in Denmark, Sweden and Scotland (Appendix A). Central populations were Tarifa (T), Camposoto (CA), Corrubedo (C), Traba (TB) and Pen Bron (F). Northern peripheral populations were Helnaes (DH), Skallingen (DS), Glommen (SG), Torekov (ST), Aberdeen (EA) and Skye (ES). Our study did not include southern peripheral populations (*i.e.*, in North Africa). All study populations contained thousands or tens of thousands of individuals, and appeared to be relatively stable in the long term (J. Villellas and M. B. García, *personal observation*). Further information of populations can be found in Villellas et al. (2012).

Data collection

We surveyed populations annually for 4 yr, yielding three annual transitions. All populations were sampled from 2007 to 2010, except for population F (period 2003-2006). However, we verified that the average and the variance of climatic variables at site F were similar in both sampling periods. In the first year, we established a number of randomly distributed plots in each population. We censused and mapped all the plants within plots each July (central populations) or August (peripheral populations), when fruits had matured but before seed dispersal. In each population census, we measured 100–400 individuals older than 1 yr that had been mapped in previous years. For each plant, we recorded the number of leaves and inflorescences, and the length of an average leaf and an average inflorescence. Plant size was later estimated as number of leaves × length of an average leaf, and seed production was estimated for reproductive individuals as number of inflorescences × length of an average inflorescence × number of seeds per unit of inflorescence length (calculated with a regression equation for each population). We also mapped each year all the new seedlings within plots (hereafter "yearlings").

We collected 10-cm deep soil cores from all populations and measured the percentage of organic matter content from the organic carbon (Heanes 1984). Meteorological data were obtained from the Spanish National Meteorological Agency (populations T and CA), MeteoGalicia (C and TB), MeteoFrance (F), Danish Meteorological Institute (DH and DS), Swedish Meteorological and Hydrological Institute (SG and ST) and Met Office (EA and ES). We used information from 10-20 years within the last four decades (depending on the availability) from the nearest meteorological station to each population (between 1 and 35 km away). We calculated mean annual temperature (ºC), mean annual precipitation (mm), and coefficient of variation (CV) in annual and monthly precipitation. The first year of this study we also estimated mean above-ground available area per individual (yearlings excluded) calculating Voronoi polygons on the scanned maps of plots (hereafter "resource area"; see also Villellas et al. 2012). We used resource area as an inverse proxy for intraspecific competition.

Projection matrices and stochastic growth rates

Individuals were classified into four stages based on age and size: one stage of yearlings (y) for plants younger than 1 yr, and three size stages (1, 2 and 3) for older plants. We used the same thresholds for size stages across populations in order to produce as even a distribution of individuals across stages as possible (see above for details on calculation of plant size, estimated from total leaf length): size $\leq 32\,\text{cm}$ (stage 1), 32 < size $\leq 50\,\text{cm}$ (stage 2), and size > 50 cm (stage 3). For most populations and years, sample sizes per size-based stage remained between 10 and 400 individuals, and in the case of yearlings between 25 and 1500 individuals. To construct projection matrices, we calculated 21 stage-specific vital rates for three annual transitions and eleven populations, for a total of 33 matrices (Fig. 1; Appendix B). Vital rates were: survival (s); probability of growing to any larger size class conditional on surviving (g); probability of growing two size classes conditional on surviving and growing (k); probability of shrinking to any smaller size class conditional on surviving and not growing (r); probability of shrinking two size classes conditional on surviving and shrinking (h); probability of reproducing (p); seed production conditional on reproducing (f); and recruitment, *i.e.* the proportion of seeds giving rise to yearlings the following year (z). Recruitment was estimated on each plot as the number of yearlings divided by the number of seeds produced in the previous year, and then averaged across plots, as recruitment from the seed bank is negligible in this species (Waite and Hutchings 1979, R. Braza and M. B. García, *unpublished data*).

Raw estimates of vital rates vary annually due both to environmental variation and to sampling variation (Gould and Nichols 1988). As our goal was to assess how much true demographic variation due to environmental fluctuations contributes to population differences in growth rates, we corrected the raw vital rate estimates for sampling error with mixed models that contained only a random effect of year (cf. Altwegg et al. 2007, Morris et al. 2011). Specifically, we corrected normally distributed vital rates (seed production) using linear mixed models, and the other rates with generalized linear mixed models, assuming binomial errors (*lme* and *lmer* procedures, packages *nlme* and *lme4*, respectively; R Development Core Team 2011). This procedure produces annual vital rate estimates that are "shrunken" toward the multi-year mean value in years with low sample sizes. Accounting for sampling variation avoids overestimating the contribution of the vital rates variabilities (Gould and Nichols 1988).

Following Caswell (2001), we calculated stochastic growth rates by projecting each population 50000 yr using random draws from the set of three annual matrices, assuming identical and independent distribution. To calculate 95% confidence intervals (CI) on stochastic growth rates, we generated 5000 bootstrap replicates for each population and identified the 2.5th and 97.5th percentiles of the distribution of growth rates. To test for differences in stochastic growth rates between central and peripheral populations, we performed a Mann-Whitney test (*wilcox.test* procedure, package *stats* in R) because we could not assume a normal distribution.

SLTRE analyses

To evaluate the contributions of the differences among populations in vital rates to the differences in stochastic growth, we carried out SLTRE analyses (Davison et al. 2010), but based on underlying vital rates rather than matrix elements (Jacquemyn et al. 2012). We performed SLTREs *between* central and peripheral regions of *P. coronopus* (hereafter SLTRE^b) and *within* both regions (hereafter SLTRE^w). In the central SLTRE^w, we analyzed differences among the five central populations, comparing them to a central reference population (CR); in the peripheral SLTRE^w, we compared the six peripheral populations to a peripheral reference population (PR); in the SLTRE^b, we compared CR and PR to a grand reference population (GR). To construct CR and PR annual matrices, we averaged annual vital rates across central and peripheral

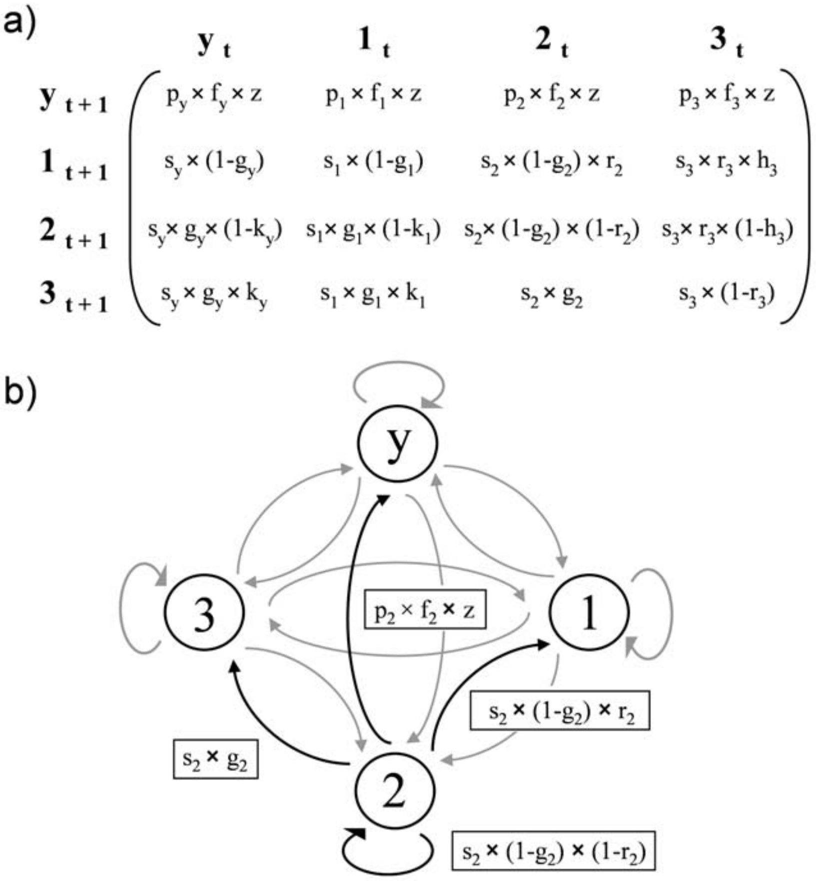

Figure 1 Projection matrix (a) and life cycle (b) of *Plantago coronopus*, with transitions between stages of one year (t) and the next (t +1). Individuals were classified into four classes: yearlings (y) and three size classes (1, 2 and 3). Vital rates, with subindices according to classes, correspond to: survival (*s*); probability of growing to any larger size class conditional on surviving (*g*); probability of growing two size classes conditional on surviving and growing (*k*); probability of shrinking to any smaller size class conditional on surviving and not growing (*r*); probability of shrinking two size classes conditional on surviving and shrinking (*h*); probability of reproducing (*p*); seed production conditional on reproducing (*f*); and recruitment, *i.e.* the proportion of seeds giving rise to yearlings the following year (*z*). All life cycle transitions were recorded in this study, but only the calculation of those starting from class 2 is detailed in b).

populations, respectively. To construct GR annual matrices, we averaged the mean annual vital rates from CR and PR. For all the reference and study populations, we calculated means and standard deviations of all vital rates across years (Davison et al. 2010). We then computed for each SLTRE the contribution of each vital rate's mean (C_m) and standard deviation (C_{sd}). For each vital rate and study population, C_m was calculated as $C_m = \left(x^P - x^R\right) \times S_m$, where x^P is the vital rate's mean in the study population, x^R is the vital rate's mean in the corresponding reference population, and S_m is the sensitivity of the reference population's stochastic growth rate to changes in the vital rate's mean. Similarly, C_{sd} 's were calculated as $C_{sd} = \left(x^P - x^R\right) \times S_{sd}$, where the x's are now vital rate standard deviations and S_{sd} is the stochastic sensitivity to changes in vital rate's standard deviation. We calculated S_m and S_{sd} using the perturbation method of Tuljapurkar et al. (2003) modified for vital rates (cf. Morris et al. 2006).

To facilitate interpretation we grouped the vital rate contributions into contributions of five life cycle components: fecundity (C_m^{Fe} and C_{sd}^{Fe}, which contain the sum of C_m and C_{sd}, respectively, of vital rates f and p), growth (C_m^{Gr} and C_{sd}^{Gr}, for rates g and k), shrinkage (C_m^{Sh} and C_{sd}^{Sh}, for rates r and h), survival (C_m^{Su} and C_{sd}^{Su}, for rate s) and recruitment (C_m^{Re} and C_{sd}^{Re}, for rate z). Then, we calculated across populations the percentage contribution of means (% C_m) and standard deviations (% C_{sd}) for each life cycle component, relative to the sum of absolute values of all contributions (Appendix C).

Relationship between population dynamics and environmental factors

To test whether populations showing demographic differences also differed in environmental conditions, we grouped them within central and peripheral areas according to the pattern of vital rate contributions (see Results). Groups C1 (T, CA and F) and C2 (C and TB) contained central populations, and groups P1 (DH, DS, ST and EA) and P2 (SG and ES) contained peripheral populations. The environmental variables analyzed were: mean annual temperature (hereafter "temperature"), mean annual precipitation (hereafter "mean precipitation"), CV in monthly precipitation (hereafter "precipitation variability"), soil organic matter content and resource area. CV in annual precipitation was discarded due to its similarity to CV in monthly precipitation and its lower correlation with demographic differences. To evaluate how the environmental variables explained demographic differences among groups, we performed a Linear Discriminant Analysis (*lda* procedure, package *MASS* in R). We tested the significance of differences among groups regarding environmental variables with a Wilks' lambda test (*manova* procedure, package *stats* in R).

Results

Stochastic growth rates

Populations showed large differences in stochastic growth rate within regions, ranging from 0.53 (population F) to 1.01 (C) in the central area and from 0.57 (DS) to 1.11 (ST) in the peripheral area (Fig. 2). For all populations, 95% confidence intervals of growth rates were narrower than ± 0.01. Nine of the 11 populations showed stochastic growth rate values below one. We found no significant differences in stochastic growth rates between central and peripheral populations (Mann-Whitney test; W = 15, p = 1).

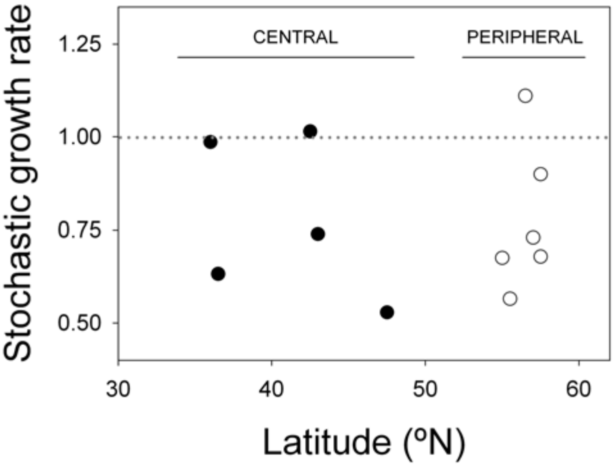

Figure 2 Stochastic growth rates in central and peripheral populations of *Plantago coronopus*. Confidence intervals are too small to be shown (see Results). Dotted line corresponds to stochastic growth rate of one.

SLTRE analyses

Stochastic sensitivities

For the three reference populations (GR, CR and PR), the vital rates' S_m were on average *ca.* 10 times higher in absolute value than their corresponding S_{sd} values (Appendix D, Fig. D1), indicating that the stochastic growth rate of these populations is far more sensitive to the average than to temporal variability in performance. S_m was positive for all rates except for the shrinkage rates r_2, r_3 and h_3. Most S_{sd} were instead negative, showing that demographic fluctuations had an overall detrimental effect on population growth, although some vital rates, such as p_y and p_3, showed positive S_{sd}. Recruitment was the vital rate with by far the highest S_m and S_{sd} in absolute value in the three reference populations, followed by yearling vital rates (s_y, p_y and g_y). Differences in vital rates' means and standard deviations between study populations and their corresponding reference population are shown in Appendix D, Table D1.

Contributions of single vital rates

In all SLTRE analyses (both between and within central and peripheral regions), C_m of vital rates was much larger than C_{sd} in absolute value (Appendix D, Figs. D2 and D3), which indicates that temporal variability of vital rates played a much smaller role than mean values in explaining spatial variability in stochastic population growth rates. Recruitment was always the rate with the highest C_m (Appendix D, Fig. D2). In addition, yearlings showed higher C_m than other stages in survival (s) and growth rates (g, k), whereas in fecundity rates (f, p) the highest C_m corresponded either to stage 3 or to yearlings. There was less consistency among the three SLTREs regarding C_{sd} of vital rates, although recruitment and yearling survival tended to show the highest values in all three analyses (Appendix D, Fig. D3).

Contributions of life cycle components

In the SLTRE^b, fecundity and recruitment showed by far the largest percentage contribution of mean values, and shrinkage the lowest (Fig. 3a). In CR, $\% C_m^{Fe}$ was positive and $\% C_m^{\mathrm{Re}}$ was negative, and the net contribution of mean values was slightly positive, whereas in PR the opposite pattern was found. The net contribution of standard deviation values was positive in CR and negative in PR, recruitment making the largest contribution (Fig. 3d). The percentage contributions of the variabilities of the other life cycle components were smaller due to low sensitivities in the case of growth (Appendix D, Fig. D1), and to opposition between positive and negative contributions in survival and fecundity (results not shown).

In the SLTRE^w analyses, recruitment had in general the largest percentage contributions of mean values (Fig. 3b, c). Two differentiated groups of populations emerged both in the central and peripheral areas: in three central populations (T, CA and F; group C1) and four peripheral populations (DH, DS, ST and EA; group P1), $\% C_m^{Gr}$ and $\% C_m^{Sh}$ were generally positive, and $\% C_m^{\mathrm{Re}}$ and $\% C_m^{Su}$ were negative; the remaining two central (C and TB; group C2) and two peripheral populations (SG and ES; group P2) generally showed the opposite pattern (with a few exceptions with respect to growth or survival). Equivalent patterns of differentiation among populations in life cycle components were thus found within both regions. Survival, fecundity and recruitment showed the largest percentage contributions of variability (Fig. 3e, f).

Population dynamics and environmental factors

In the Linear Discriminant Analysis, temperature loaded most strongly on the first axis, which explained 92 % of the differences in environmental conditions among the four groups identified in Figure 3, followed by soil organic matter, precipitation variability and resource area (Fig. 4, Appendix E). The second axis explained 7 % of the spatial variation, and was mainly determined by mean precipitation and to a lesser extent by precipitation variability. Central populations (groups C1 and C2) differentiated from peripheral populations (groups P1 and P2) along the first axis, showing higher temperatures and lower soil organic matter. Groups of populations that were defined within regions on the basis of demographic performance were instead separated along the second axis: populations from groups C1 and P1 showed lower mean precipitation and higher precipitation variability than populations from groups C2 and P2. Differences among groups regarding the environmental variables under study were significant (Wilks' lambda = 0.10, $F_5 = 9.38$, $p = 0.014$).

Discussion

In our study across the European latitudinal range of the widespread *Plantago coronopus*, we found large intraspecific variation in stochastic demography both at continental and regional scales. Despite that variation, we can formulate some general patterns. Some vital rates showed lower mean values and greater variability in peripheral than in central populations, but led to no significant differences in stochastic growth rates between regions. Although different life cycle components accounted for differences in population dynamics depending on spatial scale, recruitment was the vital rate with the highest contribution both between and within central and peripheral regions. Our results also showed that demographic variation among populations seemed to be related with differences in temperature at the continental scale, whereas it was correlated with variation in precipitation regime within both central and peripheral areas.

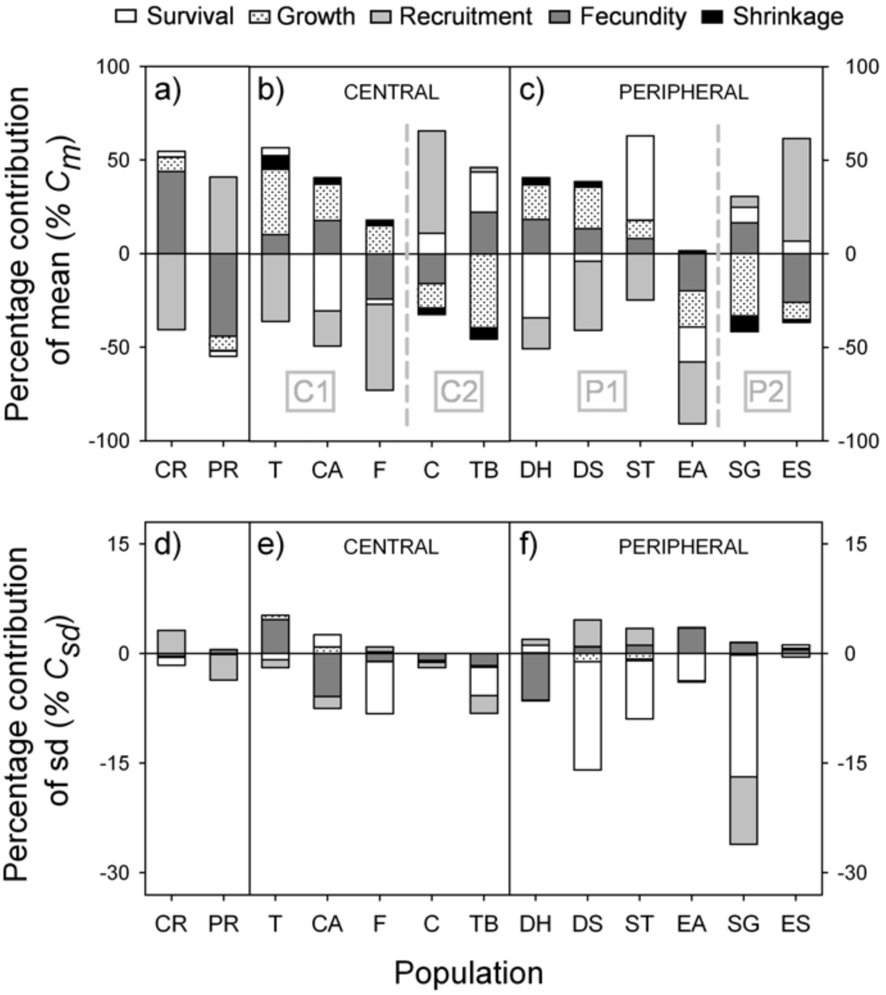

Figure 3 Percentage contributions of differences in mean values (% C_m) and standard deviation values (% C_{sd}) of vital rates of *Plantago coronopus*, grouped into life cycle components: survival, growth, recruitment, fecundity and shrinkage. Results from the SLTRE between central and peripheral regions (a, d), and from the SLTRE within central (b, e) and within peripheral (c, f) regions. Percentage contributions may be positive or negative, but the sum of absolute values of % C_m and % C_{sd} of all life cycle components must be 100 for each population. In b) and c), the dashed line separates groups of populations (C1, C2, P1 and P2) with different patterns in contributions. Note the difference in scale in Y-axis between top and bottom graphics. See Methods for population acronyms.

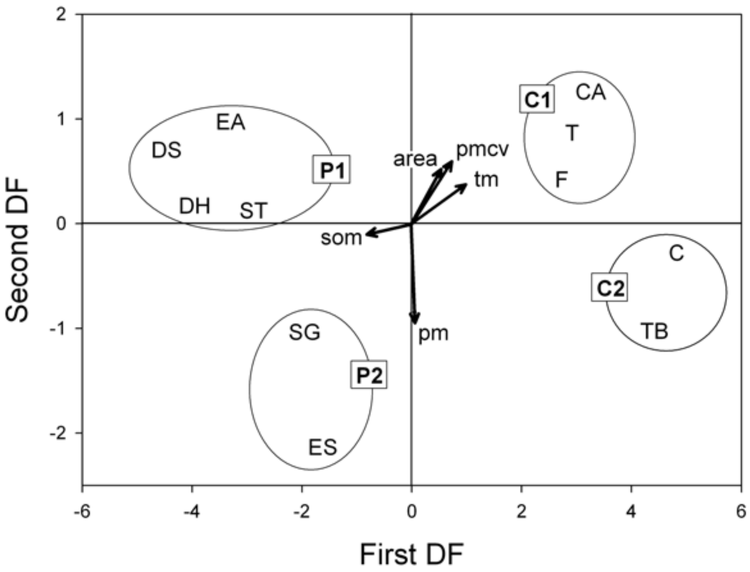

Figure 4 Canonical correlations of environmental variables from the Linear Discriminant Analysis in *Plantago coronopus*, indicating their contribution to the first and second discriminant function (arrows). Variables are mean annual temperature (tm), mean annual precipitation (pm), coefficient of variation in monthly precipitation (pmcv), soil organic matter content (som) and resource area as an inverse proxy for intraspecific competition (area). The position of populations (see Methods for population acronyms) according to their corresponding group centroids is also shown. Note the separation among population groups (C1, C2, P1, P2) between regions (left-right) and within regions (top-bottom).

Variation in population dynamics across spatial scales

We found no significant differences in stochastic growth rates between central and peripheral populations, which contrasts with classical predictions of a generalized reduction in population performance in the range periphery (Lawton 1993, Lesica and Allendorf 1995). Other recent studies have failed to find decreased growth rates towards range margins, using both deterministic (Stokes et al. 2004, Kluth and Bruelheide 2005, Eckstein et al. 2009) and stochastic approaches (Angert 2009, Doak and Morris 2010, García et al. 2010). Indeed, although multiple studies have shown reduced values in some demographic parameters at range edges, such as density or some vital rates (e.g. Carey et al. 1995, García et al. 2000, Tremblay et al. 2002), few have reported a worse overall performance in terms of population growth rates (Nantel and Gagnon 1999, Angert 2009, Eckhart et al. 2011).

Irrespective of their position, most populations in our study showed stochastic growth rates lower than one, which deserves some attention. Deviation from equilibrium in population growth is indeed typical of short-lived plants (García et al 2008). Populations of *P. coronopus* can be relatively transient in space (J. Villellas and M. B. García, *personal observation*), such that plant patches that established and grew in a certain year may decline following a perturbation, or invasion of more competitive taxa in the following years. However, the species may compensate for such declines by spreading to nearby sites within the same locations. Thus, although permanent plots are often set up in places where plants are relatively dense, the situation can change over years for short-lived species, given the large fluctuations in local populations they commonly experience (Glazier 1986). Buckley et al. (2010) also referred to the potential problems of choosing “good sites” within populations at the beginning of demographic studies.

Numerous studies to date have analyzed temporal variability in vital rates across ranges, with contrasting results. A previous study with *P. coronopus* showed higher temporal variability in peripheral than in central populations in some life cycle components, such as recruitment, and lower fluctuations in others, such as fecundity, but differences were not statistically significant (Villellas et al. 2012). Studies with other plant taxa showed higher temporal variability in vital rates in peripheral populations (Nantel and Gagnon 1999, Vucetich and Waite 2003, Gerst et al. 2011), in central populations (Kluth and Bruelheide 2005), or failed to find any clear pattern (Angert 2009). However, to our knowledge, this is the first study that quantifies the real effect on population growth rates of such differences across ranges, discounting as well for sampling variation to reduce the implicit overestimation of temporal variability. In *P. coronopus*, the overall effect of temporal variability was slightly negative for the population growth of peripheral populations, and originated almost exclusively from differences in recruitment variability. The contribution of variation in other life cycle components was negligible due to low sensitivity values or opposition between positive and negative contributions.

In all the SLTREs performed, vital rate means showed in general higher sensitivities and greater contributions to differences in population growth rates than did temporal variability, as expected (Davison et al. 2010, Jacquemyn et al. 2012). However, the net contribution of the mean values of all vital rates together was lower than that of the standard deviations in three populations in the within-region SLTREs (central TB, and peripheral DS and SG; Fig. 3). In these populations, positive and negative contributions of mean vital rates cancelled each other, whereas contributions of standard deviations did not. This result highlights the importance of considering stochasticity, and not only mean performance, when assessing demographic differences among populations (Gillespie 1977, Tuljapurkar et al. 2003, Davison et al. 2010).

Previous studies in *P. coronopus* had already suggested a key role of recruitment (Waite 1984, Braza and García 2011). Our analyses of sensitivities and contributions showed that, irrespective of the spatial scale of comparison, recruitment was indeed the most relevant vital rate for stochastic population growth. The importance of the early stages in the life cycle of *P. coronopus* was further confirmed by the high sensitivities and contributions of vital rates (*e.g.* survival) of newly recruited yearlings. Similar results were found in the short-lived congener *P. lanceolata* (van Groenendael and Slim 1988) and in other short-lived perennials (Pico et al. 2003, García et al. 2008, Davison et al. 2010), whereas population dynamics in the longer-lived congener *P. media* were more influenced by survival of the oldest stages (Eriksson and Eriksson 2000).

Despite a consistently high relevance of recruitment for the population dynamics of *P. coronopus*, we found that the set of life cycle components contributed in distinct ways to differences in population growth rates depending on the spatial scale of analysis. At continental scale, the present work confirmed previous findings (Villellas et al. 2012) that fecundity (higher in central populations) and recruitment (higher in peripheral locations) underlie demographic differences between the core and the northern edge of the species' range. Within central and peripheral regions, in contrast, there was a more balanced contribution of different life cycle components: recruitment showed the highest contribution, but growth, survival and fecundity were also relevant. Similarly, Jongejans et al. (2010) found in three perennial plants that, although a single vital rate was the most important for differences in deterministic population growth rates both between and within regions, the role of the remaining vital rates varied across scales. Changes in the relative importance of vital rates can also be found among nearby populations (Morris and Doak 2005), which indicates that the importance of life cycle components may vary within plant taxa even at small spatial scales.

The role of environmental conditions in life cycle variation

Differences in population dynamics across the range of *P. coronopus* are better understood when accounting for variation in environmental conditions. In the central-peripheral comparison, demographic differences seem to be correlated with temperature, and secondarily with other factors such as soil conditions or precipitation, although direct causal relationships are difficult to establish. Within central and peripheral areas, in contrast, demographic differences were clearly associated with precipitation regime: in both regions, populations with positive contributions of recruitment and survival, and negative contributions of growth and shrinkage (groups C2 and P2) showed higher and more constant precipitation, whereas populations with the opposite demographic pattern (groups C1 and P1) showed lower and more variable rainfall. These differences among populations seem to be reflected in additional demographic and morphological parameters analyzed elsewhere, as populations from wetter locations present higher densities and lower plant sizes than populations from drier sites (Villellas et al. 2012). Higher densities in wetter locations are likely the result of high recruitment. In turn, a negative effect of higher intraspecific competition on plant growth would result in lower plant sizes. Individual plant growth is indeed lower on average (and shrinkage higher) in these wetter sites.

The effects of environmental conditions on demography across distribution ranges seem to vary among taxa, and results from other studies differ from those presented here for *P. coronopus*. Among populations of the widespread *Stipa capillata*, for example, differences in plant performance are driven by climate in core areas and by soil conditions in the northwestern periphery (Wagner et al. 2011). In *Silene regia*, regional differences in population growth rates seem to respond in part to differences in the frequency of summer droughts, although variation in fire regime has an overall higher effect across the species' range (Menges and Dolan 1998). In the context of global change, studies such as these that relate demography and environmental conditions at different spatial scales may become powerful tools to assess current and future population performance throughout species' distributions (Jongejans et al. 2010).

To conclude, the large variation found in the life cycle of *P. coronopus* did not lead to diminished performance of any group of populations across the species' range as measured by stochastic growth rates. Instead, compensatory changes in vital rates among populations allow life cycle adjustments to regional and local environmental conditions. Similar shifts in the role of vital rates have been also documented among populations of other plant species along environmental or geographical gradients (Elderd and Doak 2006, Doak and Morris 2010). This flexibility in the life cycle appears to be common in widespread plants, and would explain the success of these taxa across large and environmentally heterogeneous ranges. Further research would be needed to determine whether the demographic differences we have observed across the range reflect phenotypic plasticity vs. local adaptation in response to spatially varying selection on life history traits.

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SUPPLEMENTAL MATERIAL

Appendix A Map showing the location of populations sampled in the study.

Appendix B Vital rate mean values for each population and transition.

Appendix C Description of calculation of percentage contribution of mean and standard deviation values of life cycle components.

Appendix D Components of SLTRE: stochastic sensitivities, differences in vital rates between study and reference populations and contributions of single vital rates.

Appendix E Environmental variables in sampled populations and canonical correlations of environmental variables from the Linear Discriminant Analysis.

APPENDIX A Map showing the location of populations sampled in the study.

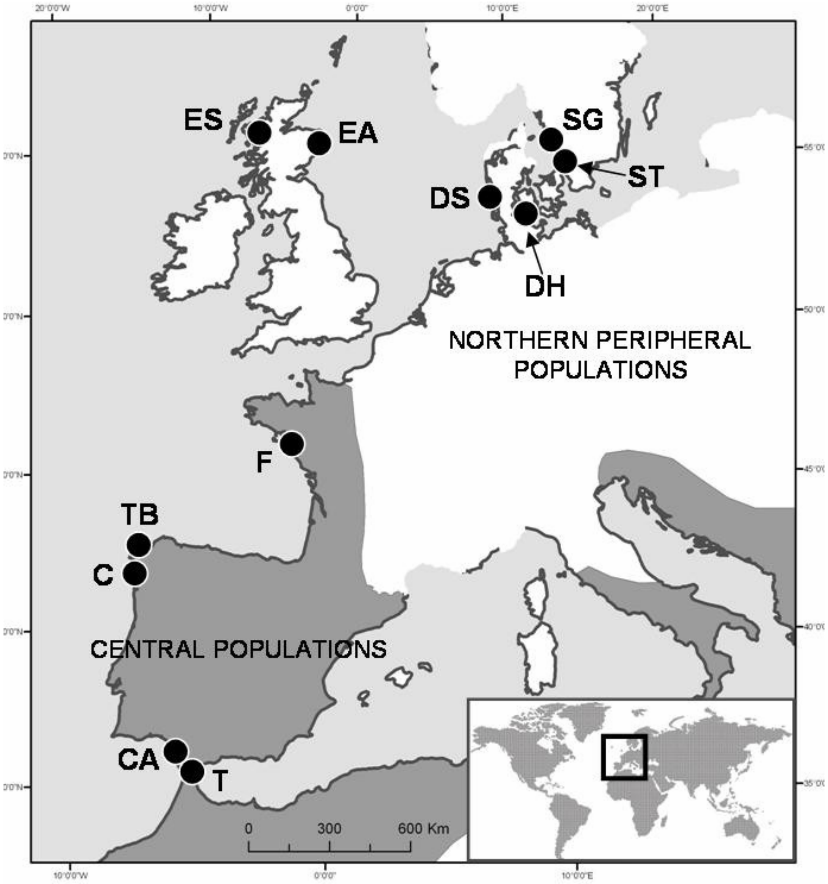

FIG. A1 Location of central and northern peripheral populations of Plantago coronopus sampled in the study (black dots; from Villellas et al. 2012). The distribution range of the species, according to Hultén and Fries (1968), is highlighted in grey (including coastal outlines in dark grey). Central populations are Tarifa (T), Camposoto (CA), Corrubedo (C), Traba (TB) and Pen Bron (F); peripheral populations are Helnaes (DH), Skallingen (DS), Glommen (SG), Torekov (ST), Aberdeen (EA) and Skye (ES).

APPENDIX B Vital rate mean values for each population and transition. Vital rates, with subindices according to classes (y: yearlings; 1, 2 and 3: three classes of increasing size), correspond to: survival (*s*); probability of growing to any larger size class conditional on surviving (*g*); probability of growing two size classes conditional on surviving and growing (*k*); probability of shrinking to any smaller size class conditional on surviving and not growing (*r*); probability of shrinking two size classes conditional on surviving and shrinking (*h*); probability of reproducing (*p*); seed production conditional on reproducing (*f*); and recruitment, *i.e.* the proportion of seeds giving rise to yearlings the following year (*z*). The number of decimals shown for each vital rate depends on their magnitude.

Vital rates		**Central populations**					**Peripheral populations**					
		T	CA	F	C	TB	DH	DS	ST	EA	SG	ES
TRANSITION 1	s_y	0.2290	0.2482	0.1111	0.6054	0.6435	0.1593	0.1929	0.8551	0.0739	0.8330	0.0931
	g_y	0.5519	0.9829	0.1982	0.1852	0.0540	0.8008	0.1192	0.6561	0.2283	0.0940	0.0949
	k_y	0.5871	0.8552	0.5000	0.2895	0.3055	0.6438	0.5000	0.4694	0.5172	0.2000	0.2774
	f_y	419.4	583.1	132.5	128.6	155.7	51.9	146.8	0.0	0.0	0.0	0.0
	p_y	0.0735	0.7519	0.1208	0.1080	0.0734	0.4832	0.0087	0.0000	0.0000	0.0000	0.0000
	z	0.0004	0.0001	0.0005	0.0043	0.0049	0.0206	0.0082	0.0229	0.0341	0.0851	0.1292
	s_1	0.2781	0.3125	0.1391	0.5066	0.8360	0.2413	0.4404	0.4930	0.5594	0.6702	0.6550
	g_1	0.5908	0.6000	0.6320	0.3145	0.1581	0.5556	0.4184	0.7649	0.1814	0.2712	0.2083
	k_1	0.6654	0.9591	0.6000	0.3467	0.2759	0.8089	0.4720	0.3399	0.3902	0.1683	0.1594
	f_1	460.1	468.1	220.3	264.0	184.9	79.1	80.0	102.9	84.0	95.4	51.1
	p_1	0.5167	0.1249	0.2333	0.2167	0.3879	0.0089	0.0524	0.1538	0.1210	0.2619	0.0895
	s_2	0.5484	0.4414	0.1238	0.6366	0.7827	0.2857	0.6386	0.6560	0.6116	0.6675	0.7372
	g_2	0.6274	0.9993	0.8000	0.2186	0.1360	0.3571	0.4877	0.4139	0.2212	0.0551	0.2378
	r_2	0.4210	0.7500	0.0000	0.4549	0.6590	0.7619	0.3846	0.3322	0.5185	0.7000	0.6125
	f_2	578.1	1562.0	323.6	618.6	785.0	76.6	255.1	158.0	86.2	151.7	59.2
	p_2	0.5265	0.0000	0.5818	0.6884	0.7801	0.1908	0.4000	0.5341	0.3614	0.6493	0.2619
	s_3	0.4732	0.4530	0.2323	0.6624	0.8625	0.2257	0.8435	0.6718	0.6295	0.6653	0.7358
	r_3	0.1467	0.0833	0.4682	0.7699	0.5394	0.1622	0.3333	0.3361	0.3907	0.8427	0.6026
	h_3	0.4000	0.4000	0.4167	0.4828	0.6422	0.3333	0.4287	0.3606	0.4833	0.6800	0.6383
	f_3	1519.1	1496.7	838.6	1310.3	2471.6	225.5	351.7	234.6	273.6	357.0	136.3
	p_3	0.9369	0.9007	0.8512	0.9175	0.9866	0.9286	0.6486	0.7687	0.6117	0.8382	0.2489
TRANSITION 2	s_y	0.5074	0.2363	0.9912	0.4879	0.4076	0.2159	0.6363	0.4725	0.0441	0.1791	0.2300
	g_y	0.7240	0.8515	0.6426	0.3240	0.0334	0.4701	0.6270	0.2428	0.0619	0.0340	0.1785
	k_y	0.6869	0.8499	0.5000	0.2895	0.3055	0.6438	0.5000	0.3169	0.5172	0.2000	0.3232
	f_y	286.9	560.5	132.5	316.6	346.8	270.4	146.8	0.0	0.0	0.0	0.0
	p_y	0.3990	0.4236	0.0296	0.0162	0.0061	0.0106	0.0657	0.0000	0.0000	0.0000	0.0000
	z	0.0019	0.0004	0.0005	0.0057	0.0012	0.0236	0.0040	0.0095	0.0124	0.0190	0.1108
	s_1	0.5574	0.3125	0.4214	0.3728	0.5739	0.2852	0.7500	0.7456	0.4154	0.6132	0.7487
	g_1	0.5627	0.6000	0.9933	0.6017	0.1237	0.5556	0.7672	0.4683	0.1814	0.1421	0.2083
	k_1	0.6443	0.5285	0.6000	0.3467	0.2759	0.6405	0.6262	0.3399	0.3902	0.1683	0.3192
	f_1	460.1	468.1	220.3	247.5	424.6	79.1	80.0	134.2	84.0	102.8	39.7
	p_1	0.7651	0.1514	0.2333	0.7078	0.6742	0.0112	0.0317	0.2316	0.1299	0.2619	0.0992
	s_2	0.5484	0.3293	0.4128	0.4229	0.7116	0.2857	0.7309	0.8112	0.5517	0.6100	0.8090
	g_2	0.6274	0.0000	0.8000	0.3096	0.0646	0.3571	0.7489	0.2969	0.2212	0.0551	0.3580
	r_2	0.4210	0.7500	0.0000	0.4438	0.6341	0.1111	0.3846	0.5034	0.5185	0.7000	0.6125
	f_2	578.1	1562.0	323.6	464.1	1071.6	76.6	193.5	180.4	115.0	153.3	62.1
	p_2	0.8772	0.9985	0.5818	0.9685	0.9727	0.3713	0.3764	0.5565	0.3614	0.6493	0.1615
	s_3	0.4732	0.1626	0.3351	0.4664	0.6970	0.5533	0.9935	0.8841	0.4773	0.5260	0.7358
	r_3	0.0854	0.0833	0.2283	0.7699	0.8425	0.1622	0.3333	0.6367	0.3907	0.8427	0.6026
	h_3	0.4000	0.4000	0.4167	0.4828	0.6422	0.3333	0.2709	0.3606	0.4994	0.6800	0.6383
	f_3	1519.1	3156.6	1279.9	885.5	2575.2	389.3	351.7	319.8	273.6	266.5	66.1
	p_3	0.9369	0.9542	0.8512	0.9175	0.9866	0.9286	0.6486	0.8357	0.2622	0.8695	0.2196
TRANSITION 3	s_y	0.3676	0.1917	0.2422	0.3369	0.1560	0.0874	0.0451	0.2732	0.3450	0.1547	0.3531
	g_y	0.7644	0.5134	0.8128	0.2388	0.0437	0.2983	0.6542	0.1369	0.0810	0.0163	0.0714
	k_y	0.7296	0.7396	0.5000	0.2895	0.3055	0.6438	0.5000	0.3394	0.5172	0.2000	0.2512
	f_y	268.9	258.6	132.5	66.2	101.4	213.5	146.8	0.0	0.0	0.0	0.0
	p_y	0.0274	0.1769	0.0653	0.1110	0.0970	0.0247	0.0077	0.0000	0.0000	0.0000	0.0000
	z	0.0022	0.0036	0.0005	0.0070	0.0010	0.0029	0.0034	0.0112	0.0035	0.0072	0.0924
	s_1	0.4510	0.3125	0.4697	0.3388	0.2402	0.3046	0.1006	0.4770	0.6685	0.1291	0.6658
	g_1	0.5965	0.6000	0.9917	0.4035	0.1012	0.5556	0.1704	0.4423	0.1814	0.0299	0.2083
	k_1	0.7468	0.0978	0.6000	0.3467	0.2759	0.3031	0.5491	0.3399	0.3902	0.1683	0.1548
	f_1	460.1	468.1	220.3	92.4	247.1	79.1	80.0	81.7	84.0	81.9	69.8
	p_1	0.7899	0.2177	0.2333	0.4660	0.4830	0.1025	0.0329	0.1449	0.1122	0.2619	0.0231
	s_2	0.5484	0.2381	0.3241	0.4129	0.2363	0.2857	0.0723	0.5158	0.7365	0.1137	0.6733
	g_2	0.6274	0.0000	0.8000	0.0937	0.0615	0.3571	0.7687	0.2977	0.2212	0.0551	0.2319
	r_2	0.4210	0.7500	0.0000	0.4406	0.9069	0.2667	0.3846	0.4894	0.5185	0.7000	0.6125
	f_2	578.1	1562.0	323.6	185.7	826.4	76.6	184.5	122.8	111.5	120.8	104.5
	p_2	0.8403	0.0000	0.5818	0.8099	0.9615	0.5957	0.2819	0.5402	0.3614	0.6493	0.0656
	s_3	0.4732	0.2156	0.4711	0.4446	0.3570	0.0602	0.0258	0.5197	0.7246	0.2396	0.7358
	r_3	0.2344	0.0833	0.2181	0.7699	0.7780	0.1622	0.3333	0.5423	0.3907	0.8427	0.6026
	h_3	0.4000	0.4000	0.4167	0.4828	0.6422	0.3333	0.3098	0.3606	0.4994	0.6800	0.6383
	f_3	1519.1	783.8	2005.6	415.6	1682.5	386.2	351.7	207.8	274.9	174.7	131.3
	p_3	0.9369	0.6753	0.8512	0.9175	0.9866	0.9286	0.6486	0.7816	0.5382	0.7127	0.2037

APPENDIX C Description of calculation of percentage contribution of mean and standard deviation values of life cycle components.

The percentage contribution of mean values (*% C_m*) of each life cycle component (in this case for fecundity) to differences in stochastic population growth rates was calculated as follows:

$$\%\,C_m^{Fe} = 100 \times \frac{C_m^{Fe}}{\sum_i \left|C_m^i\right| + \sum_i \left|C_{sd}^i\right|}\,, \tag{C.1}$$

where i corresponds to each life cycle component. Similarly, the percentage contribution of standard deviation values for fecundity vital rates ($\%\,C_{sd}^{Fe}$) was:

$$\%\,C_{sd}^{Fe} = 100 \times \frac{C_{sd}^{Fe}}{\sum_i \left|C_m^i\right| + \sum_i \left|C_{sd}^i\right|}\,. \tag{C.2}$$

Percentage contributions may be positive or negative, but the sum of absolute values of *% C_m* and *% C_{sd}* of all life cycle components must be 100 for each population. Percentage contributions are an appropriate method to summarize and compare population dynamics in *Plantago coronopus* since they constitute a relative measure that can be compared across populations, and because within a given life cycle component there were few cases in which positive and negative contributions of vital rates cancelled one another.

APPENDIX D Components of SLTRE: stochastic sensitivities, differences in vital rates between study and reference populations and contributions of single vital rates.

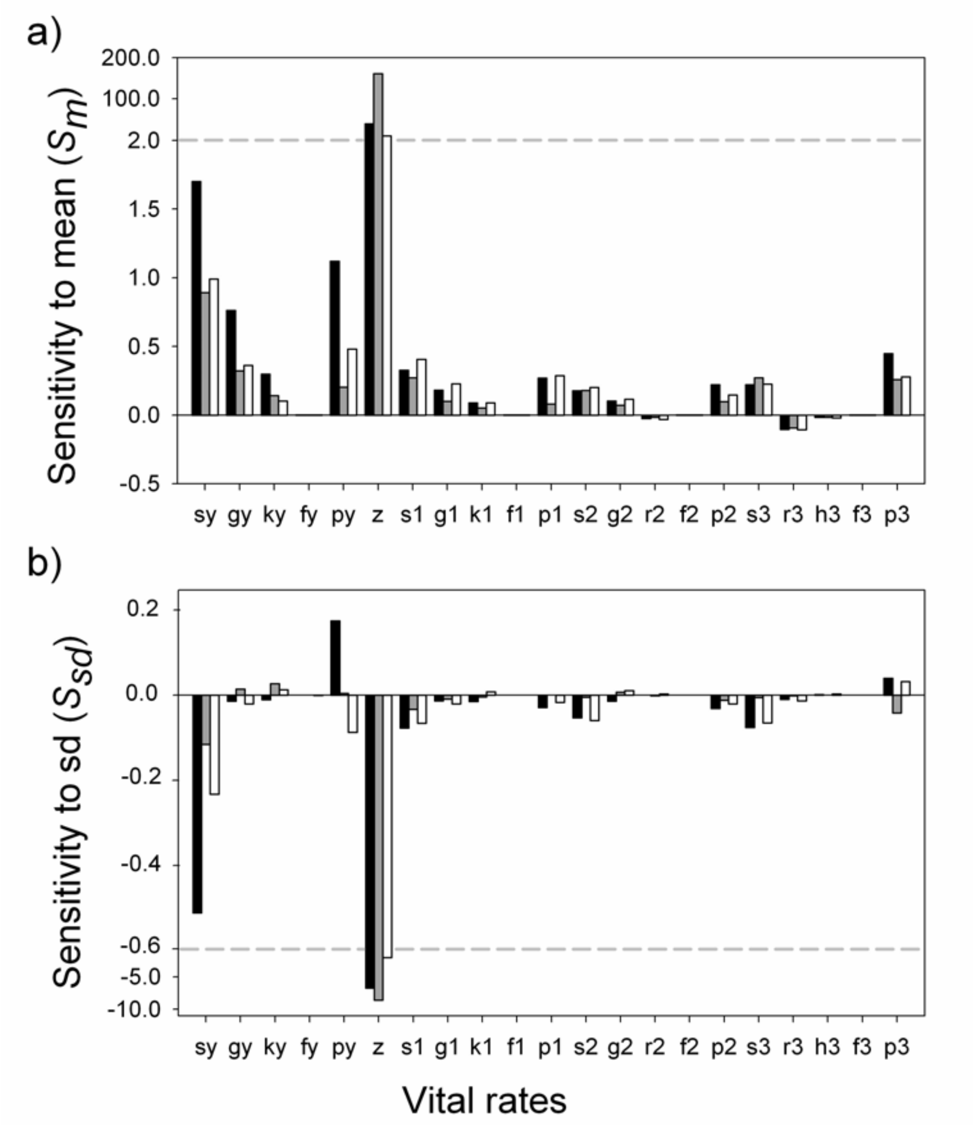

FIG. D1 Sensitivities of stochastic growth rates to changes in mean values, S_m (a), and standard deviation values, S_{sd} (b), of vital rates. Sensitivities correspond to reference populations in the three SLTRE analyses: GR (black) for the between-region SLTRE, and CR (grey) and PR (white) for the central and the peripheral within-region SLTRE, respectively. Vital rates, with subindices according to classes (y: yearlings; 1, 2 and 3: three classes of increasing size), correspond to: survival (*s*); probability of growing to any larger size class conditional on surviving (*g*); probability of growing two size classes conditional on surviving and growing (*k*); probability of shrinking to any smaller size class conditional on surviving and not growing (*r*); probability of shrinking two size classes conditional on surviving and shrinking (*h*); probability of reproducing (*p*); seed production conditional on reproducing (*f*); and recruitment, *i.e*. the proportion of seeds giving rise to yearlings the following year (*z*). Scale was changed for values > 2 (a) and values < -0.6 (b), as indicated by horizontal dashed lines, due to very high values of sensitivity for the vital rate *z*. Note the difference in scale between a) and b).

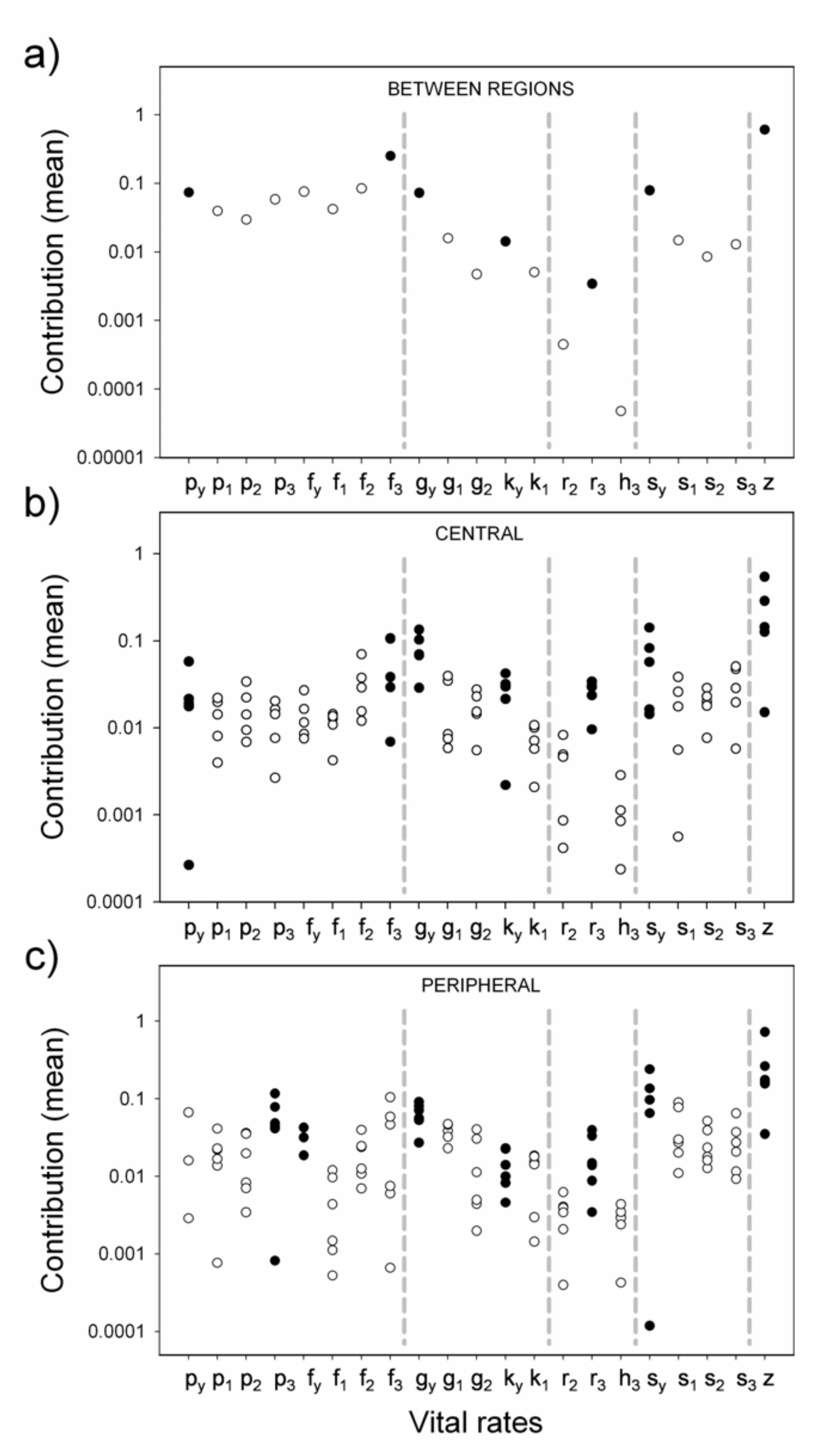

FIG. D2 Absolute values of the contributions of mean vital rates to differences in stochastic population growth rates (C_m in main text) in the SLTRE between regions (a), within the central region (b) and within the peripheral region (c). See Fig. D1 for vital rate abbreviations. Vital rates are ordered according to life cycle components, separated by dashed lines: fecundity (*p*, *f*), growth (*g*, *k*), shrinkage (*r*, *h*), survival (*s*) and recruitment (*z*). Vertical axes are log-transformed. Black dots correspond to the vital rates within each life cycle component that make the highest contributions across stages.

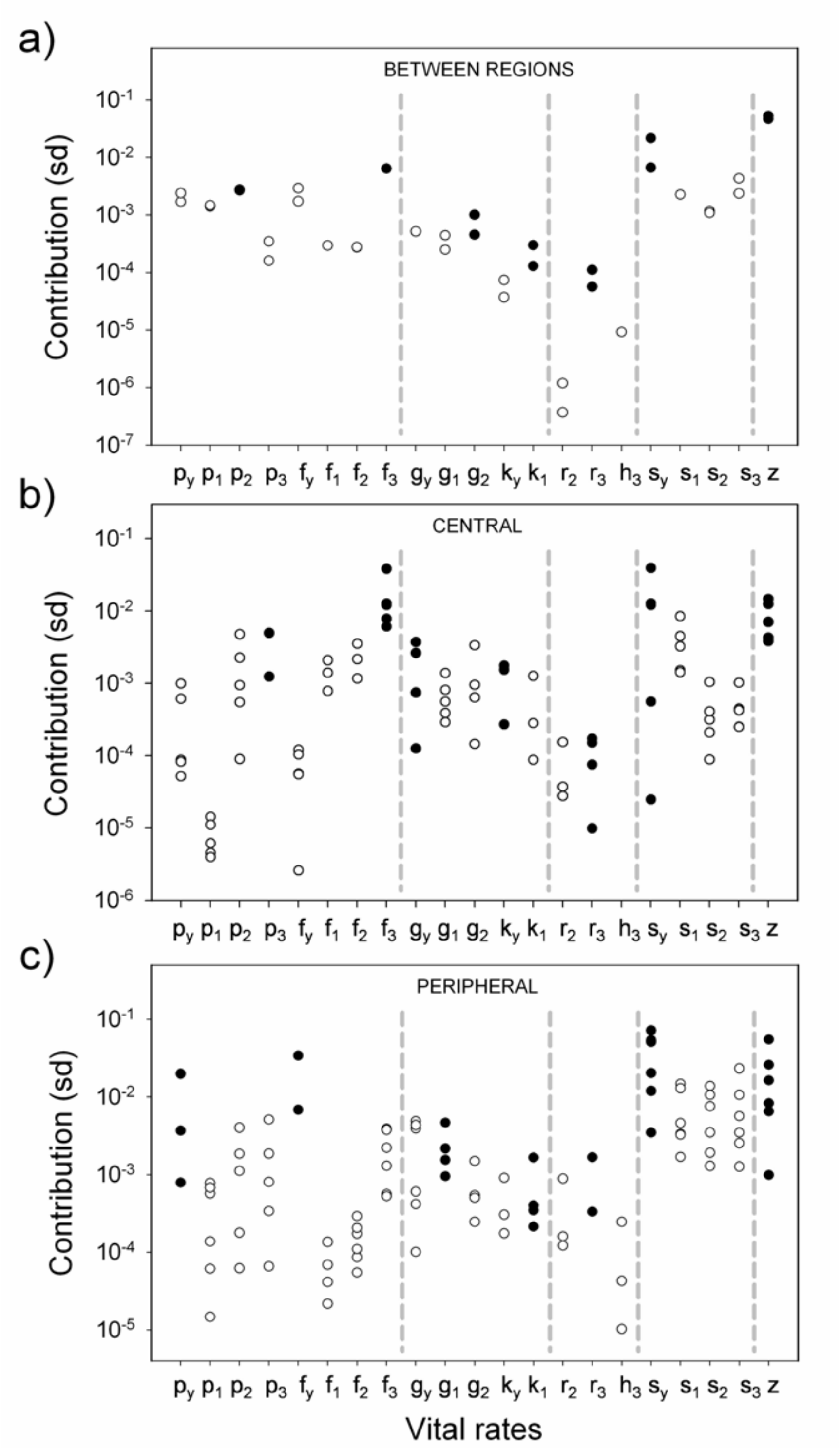

FIG. D3 Absolute values of the contributions of standard deviations (sd) of vital rates to differences in stochastic population growth rates (C_{sd} in main text) in the SLTRE between regions (a), within the central region (b) and within the peripheral region (c). See Fig. D1 for vital rate abbreviations. Vital rates are ordered according to life cycle components, separated by dashed lines: fecundity (*p*, *f*), growth (*g*, *k*), shrinkage (*r*, *h*), survival (*s*) and recruitment (*z*). Vertical axes are log-transformed. Black dots correspond to the vital rates within each life cycle component that make the highest contributions across stages. In b), C_{sd} of h_3 is zero for all populations.

TABLE D1 Differences in mean and standard deviation (sd) values of vital rates between study and reference population in the SLTREs. See Fig. D1 for vital rate abbreviations. Positive values are highlighted in bold.

Vital rates	**Between-region SLTRE**		**Within-region SLTRE**										
			Central populations					**Peripheral populations**					
	CR	PR	T	CA	F	C	TB	DH	DS	ST	EA	SG	ES
Mean													
s_y	**0.05**	-0.05	-0.02	-0.16	**0.06**	**0.09**	**0.02**	-0.14	**0.00**	**0.24**	-0.14	**0.10**	-0.07
g_y	**0.10**	-0.10	**0.22**	**0.32**	**0.09**	-0.21	-0.42	**0.25**	**0.20**	**0.07**	-0.15	-0.22	-0.16
k_y	**0.05**	-0.05	**0.15**	**0.30**	-0.02	-0.23	-0.21	**0.22**	**0.08**	-0.04	**0.10**	-0.22	-0.14
f_y	**102.6**	-102.6	**65.7**	**208.1**	-126.8	-88.9	-58.0	**124.4**	**92.6**	-54.2	-54.2	-54.2	-54.2
p_y	**0.07**	-0.07	**0.00**	**0.29**	-0.09	-0.09	-0.11	**0.14**	-0.01	-0.03	-0.03	-0.03	-0.03
z	-0.02	**0.02**	0.00	0.00	0.00	**0.00**	**0.00**	-0.02	-0.03	-0.02	-0.02	**0.00**	**0.08**
s_1	-0.04	**0.04**	**0.02**	-0.10	-0.06	0.00	**0.14**	-0.22	-0.07	**0.07**	**0.05**	-0.03	**0.19**
g_1	**0.09**	-0.09	**0.06**	**0.08**	**0.35**	-0.08	-0.40	**0.20**	**0.10**	**0.21**	-0.17	-0.20	-0.14
k_1	**0.06**	-0.06	**0.20**	**0.04**	**0.11**	-0.14	-0.21	**0.21**	**0.18**	-0.03	**0.02**	-0.21	-0.16
f_1	**122.2**	-122.2	**133.0**	**141.0**	-106.8	-125.8	-41.5	-3.62	-2.74	**23.6**	**1.29**	**10.6**	-29.2
p_1	**0.15**	-0.15	**0.28**	-0.25	-0.18	**0.05**	**0.10**	-0.08	-0.08	**0.06**	**0.00**	**0.14**	-0.05
s_2	-0.05	**0.05**	**0.10**	-0.11	-0.16	**0.04**	**0.13**	-0.26	-0.06	**0.12**	**0.09**	-0.08	**0.20**
g_2	**0.05**	-0.05	**0.22**	-0.08	**0.39**	-0.20	-0.32	**0.04**	**0.35**	**0.02**	-0.10	-0.26	-0.04
r_2	-0.02	**0.02**	-0.05	**0.28**	-0.47	-0.02	**0.26**	-0.13	-0.12	-0.06	**0.01**	**0.19**	**0.11**
f_2	**314.5**	-314.5	-178.0	**805.8**	-432.6	-333.4	**138.2**	-50.5	**83.9**	**26.6**	-22.9	**14.8**	-51.9
p_2	**0.13**	-0.13	**0.07**	-0.35	-0.10	**0.14**	**0.23**	-0.02	-0.06	**0.13**	-0.05	**0.24**	-0.25
s_3	-0.06	**0.06**	**0.02**	-0.17	-0.11	**0.07**	**0.19**	-0.29	**0.05**	**0.12**	**0.04**	-0.09	**0.17**
r_3	-0.03	**0.03**	-0.25	-0.32	-0.10	**0.36**	**0.31**	-0.31	-0.14	**0.03**	-0.08	**0.37**	**0.13**
h_3	-0.00	**0.00**	-0.07	-0.07	-0.05	**0.01**	**0.17**	-0.14	-0.14	-0.11	**0.02**	**0.21**	**0.16**
f_3	**649.4**	-649.4	-44.80	**248.4**	-189.3	-693.5	**679.2**	**68.5**	**86.6**	-11.1	**8.87**	**0.98**	-153.9
p_3	**0.13**	-0.13	**0.03**	-0.06	-0.06	**0.01**	**0.08**	**0.28**	**0.00**	**0.15**	-0.17	**0.16**	-0.42
Sd													
s_y	**0.04**	-0.01	**0.00**	-0.10	**0.34**	**0.00**	**0.11**	-0.01	**0.23**	**0.22**	**0.09**	**0.31**	**0.05**
g_y	**0.04**	**0.04**	**0.05**	**0.18**	**0.26**	**0.01**	-0.05	**0.19**	**0.24**	**0.21**	**0.03**	-0.02	0.00
k_y	**0.00**	**0.01**	**0.06**	**0.06**	-0.01	-0.01	-0.01	-0.01	-0.01	**0.07**	-0.01	-0.01	**0.02**
f_y	**41.1**	-24.3	-2.09	**96.9**	-84.3	**46.0**	**44.6**	**94.5**	-18.9	-18.9	-18.9	-18.9	-18.9
p_y	**0.01**	-0.01	**0.14**	**0.22**	-0.02	-0.01	-0.02	**0.23**	-0.01	-0.04	-0.04	-0.04	-0.04
z	-0.01	**0.01**	**0.00**	**0.00**	-0.00	**0.00**	**0.00**	-0.00	-0.01	-0.01	**0.00**	**0.03**	**0.00**
s_1	-0.03	**0.03**	**0.10**	-0.04	**0.14**	**0.05**	**0.26**	-0.07	**0.22**	**0.05**	**0.03**	**0.20**	-0.05
g_1	**0.02**	**0.03**	-0.04	-0.06	**0.15**	**0.09**	-0.03	-0.07	**0.23**	**0.10**	-0.07	**0.05**	-0.07
k_1	**0.02**	-0.01	-0.02	**0.35**	-0.08	-0.08	-0.08	**0.21**	**0.03**	-0.05	-0.05	-0.05	**0.04**
f_1	**15.1**	-15.1	-33.90	-33.9	-33.9	**60.8**	**90.5**	-3.65	-3.65	**22.8**	-3.65	**6.92**	**11.6**
p_1	**0.05**	-0.05	**0.04**	-0.06	-0.11	**0.14**	**0.04**	**0.05**	**0.00**	**0.04**	**0.00**	-0.01	**0.03**
s_2	-0.02	**0.02**	-0.08	**0.02**	**0.06**	**0.04**	**0.21**	-0.13	**0.23**	**0.02**	-0.03	**0.18**	-0.06
g_2	**0.07**	-0.03	-0.13	**0.45**	-0.13	-0.02	-0.09	-0.02	**0.13**	**0.05**	-0.02	-0.02	**0.05**
r_2	**0.01**	**0.02**	-0.03	-0.03	-0.03	-0.02	**0.12**	**0.30**	-0.04	**0.05**	-0.04	-0.04	-0.04
f_2	**24.3**	-24.0	-54.5	-54.5	-54.5	**164.9**	**100.5**	-6.09	**32.3**	**22.9**	**9.61**	**12.2**	**19.3**
p_2	**0.09**	-0.09	**0.01**	**0.39**	-0.19	-0.04	-0.08	**0.19**	**0.05**	**0.00**	-0.01	-0.01	**0.09**
s_3	-0.03	**0.06**	-0.08	**0.08**	**0.04**	**0.04**	**0.18**	**0.09**	**0.36**	**0.02**	-0.04	**0.05**	-0.16
r_3	-0.01	**0.01**	**0.07**	-0.01	**0.13**	-0.01	**0.15**	-0.03	-0.03	**0.13**	-0.03	-0.03	-0.03
h_3	-0.01	**0.01**	-0.00	-0.00	-0.00	-0.00	-0.00	-0.01	**0.07**	-0.01	-0.00	-0.01	-0.01
f_3	**145.4**	-145.4	-302.6	**914.9**	**286.6**	**144.9**	**185.6**	**81.9**	-11.8	**46.7**	-11.1	**79.3**	**27.3**
p_3	**0.01**	**0.00**	-0.03	**0.12**	-0.03	-0.03	-0.03	-0.02	-0.02	**0.01**	**0.16**	**0.06**	-0.00

APPENDIX E Environmental variables in sampled populations and canonical correlations of environmental variables from the Linear Discriminant Analysis. Canonical correlations indicate their contributions to the first and second Discriminant Functions (DF). Population acronyms are followed by their belonging group in parenthesis, according to demographic differences (see Methods for details); groups C1 and C2 contain central populations and groups P1 and P2 contain peripheral populations.

	Annual Temperature (ºC)	**Annual precipitation (mm)**	**Precipitation variability (CV)**	**Soil organic matter content (%)**	**Resource area (cm^2)**
Populations					
T (C1)	17.1	627	1.09	0.7	597.3
CA (C1)	18.7	533	1.14	0.4	347
F (C1)	12.8	678	0.66	0.9	35.8
C (C2)	14.9	1031	0.73	1.1	66.0
TB (C2)	14.4	1249	0.72	1.4	70.5
DH (P1)	8.1	567	0.59	5.6	33.9
DS (P1)	9.1	848	0.64	17.9	29.5
ST (P1)	8.8	657	0.59	6.1	17.7
EA (P1)	8.6	808	0.54	18.1	16.6
SG (P2)	8.0	850	0.51	0.8	24.6
ES (P2)	9.1	1847	0.52	17.7	6.6
Canonical correlations					
First DF	0.88	0.05	0.63	-0.70	0.47
Second DF	0.34	-0.85	0.53	-0.09	0.45

Chapter 3

The role of the tolerance-fecundity trade-off in maintaining intraspecific seed trait variation in a widespread dimorphic herb

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RESEARCH PAPER

The role of the tolerance–fecundity trade-off in maintaining intraspecific seed trait variation in a widespread dimorphic herb

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Keywords

Environmental stress gradient; latitudinal gradient; mucilage; *Plantago coronopus*; plant size; seed heteromorphism; seed number and weight; short-lived perennial.

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ABSTRACT

Coexistence of species with different seed sizes is a long-standing issue in community ecology, and a trade-off between fecundity and stress tolerance has been proposed to explain co-occurrence in heterogeneous environments. Here we tested an intraspecific extension of this model: whether such trade-off also explains seed trait variation among populations of widespread plants under stress gradients. We collected seeds from 14 populations of *Plantago coronopus* along the Atlantic coast in North Africa and Europe. This herb presents seed dimorphism, producing large basal seeds with a mucilaginous coat that facilitates water absorption (more stress tolerant), and small apical seeds without coats (less stress tolerant). We analysed variation among populations in number, size and mucilage production of basal and apical seeds, and searched for relationships between local environment and plant size. Populations under higher stress (higher temperature, lower precipitation, lower soil organic matter) had fewer seeds per fruit, higher predominance of basal relative to apical seeds, and larger basal seeds with thicker mucilaginous coats. These results strongly suggest a trade-off between tolerance and fecundity at the fruit level underpins variation in seed traits among *P. coronopus* populations. However, seed production per plant showed the opposite pattern to seed production per fruit, and seemed related to plant size and other life-cycle components, as an additional strategy to cope with environmental variation across the range. The tolerance–fecundity model may constitute, under stress gradients, a broader ecological framework to explain trait variation than the classical seed size–number compromise, although several fecundity levels and traits should be considered to understand the diverse strategies of widespread plants to maximise fitness in each set of local conditions.

INTRODUCTION

Seed production and seed traits represent crucial components in plant fitness. Seed size, for example, is closely related to important ecological and demographic processes, such as dispersal, germination or seedling survival (Westoby *et al.* 1992; Chapin *et al.* 1993; Coomes & Grubb 2003). Seed production also plays a major role in individual fitness and population persistence (Lloyd 1987; Westoby *et al.* 2002), and a trade-off between size and the number of seeds is expected (Smith & Fretwell 1974; Lloyd 1987). In addition, both seed size and total seed production might show a positive relationship with plant size (Primack 1987; Herrera 1991; Aarssen & Jordan 2001). The presence of mucilaginous seed coats in some plant species may also affect relevant seed-related processes, such as water stress tolerance, competition *via* allelopathy or adherence to soil particles (Harper & Benton 1966; Hasegawa *et al.* 1992; Lu *et al.* 2010). Many taxa present remarkable differences in seed characteristics among populations (*e.g.,* McWilliams *et al.* 1968; McKee & Richards 1996; Mendez 1997), and quantifying this intraspecific variation and determining its underlying causes may be important to understand why some plants are more successful than others in terms of colonisation or adaptation to new ecological or climate scenarios (Buckley *et al.* 2003; Wright *et al.* 2006; Albert *et al.* 2010).

Environmental stress is a crucial factor in the ecology and evolution of plants (Grime 1977; Parsons 1991; Nevo 2001), and variation in stress levels may promote seed trait divergences among or within species. The hypothesis of the tolerance–fecundity trade-off (Muller-Landau 2010; see also Westoby *et al.* 2002) has been proposed to explain the coexistence of plant species with different seed sizes in environmentally heterogeneous communities. The underlying mechanism is related to a demographic process, *i.e.* the differential probability of recruitment at the available regeneration niches. In this process, high-stress regeneration sites would be eventually occupied by large-seeded species, thanks to their higher tolerance to environmental stress. Low-stress patches, in contrast, would be occupied by species of different seed sizes and tolerances, although small-seeded species would become dominant due to their higher seed production relative to large-seeded species. Because of its logic and simplicity, the mechanism underlying the tolerance–fecundity model could be rather general, and also explain variation in seed traits across populations of species occurring along environmental stress gradients. In this intraspecific extension of the model, populations in stressful environments would provide the seeds with additional resources at the cost of reducing seed number. In contrast, populations in less stressful conditions could afford to reduce resource investment per seed (and thus stress tolerance) in order to increase offspring number. These predictions rely on the assumption that available resources for seed production are constant across populations and do not co-vary with traits involved in the trade-off (Van Noordwijk & De Jong 1986). In addition, despite that seed size is the most frequently studied trait, other seed characteristics could be considered to evaluate stress tolerance (Muller-Landau 2010), such as coat features or shape.

Widespread plants occurring along environmental gradients represent typical examples of high phenotypic variability (Joshi *et al.* 2001; Richards *et al.* 2005), and provide a good opportunity to analyse intraspecific variation in seed traits in relation to environmental conditions. *Plantago coronopus* is a common, short-lived perennial herb present along a strong environmental gradient on the eastern Atlantic coast, and shows large differences among populations in terms of fecundity (Braza *et al.* 2010; Villellas *et al.* 2012). Additionally, this taxon presents seed dimorphism (Dowling 1933; Schat 1981), whereby fruits produce both large basal seeds with a mucilaginous coat and small apical seeds without such a coat. For individuals emerging from basal seeds, plant performance (germination, survival and fecundity) is positively correlated with original seed size (Koelewijn & Van Damme 2005). Moreover, basal seeds germinate better than apical ones, especially in dry years (Braza & García 2011), which likely results from higher reserves (Chapin *et al.* 1993; Westoby *et al.* 2002; Coomes & Grubb 2003) and higher water absorption through the mucilaginous coat (Harper & Benton 1966; Gutterman & Shem-Tov 1997; Schat 1981).

In this study, we analyse variation among populations of the widespread herb *P. coronopus* in a set of seed traits, and its relationship with environmental stress. Climate has a key role in plant performance at large scales (Woodward & Williams 1987), and the positive relationship of seed size and mucilage with seed performance in this species specifically suggests water and nutrient deficits as potential sources of stress. Consequently, we tested the effect of environmental stress on seed traits using: (i) water availability, estimated both from precipitation (see also Harper & Benton 1966; Baker 1972; Wright & Westoby 1999) and a more integrative metric of water deficit considering the balance between evapotranspiration and precipitation (Thornthwaite 1948); (ii) temperature, which may reduce water availability (Baker 1972) or directly affect plant metabolic processes, as seeds require more energy to grow into seedlings under warmer conditions (Lord *et al.* 1997; Murray *et al.* 2004); and (iii) soil organic matter content, which can be used as an indicator of soil fertility (Reeves 1997) and may also be associated with soil water retention due to small particle sizes and high cation exchange capacity (Cobertera 1993).

To analyse variation in fecundity and seed traits in *P. coronopus*, we sampled 14 populations along the Atlantic coast of North Africa and Europe, spanning a latitudinal gradient of 4000 km. Here, we first report variability among populations in the number, size and production of mucilage in basal and apical seeds. Given that *P. coronopus* is a perennial plant, we consider fecundity at three levels: per individual over the lifespan, per individual per year, and per fruit. Second, we analyse if seed trait variation is associated with soil and climate conditions, considering low water availability, high temperature and low organic matter content as representative of stressful conditions. We also analyse if seed trait variation is affected by plant size. Third, we test whether a trade-off between fecundity (at the three levels) and stress tolerance promotes diversity in seed traits among populations of this dimorphic species. In that case, we would expect populations subject to higher stress to present: (i) a higher predominance of basal (more stress-tolerant) relative to apical (less stress-tolerant) seeds; (ii) larger basal seeds with higher mucilage production; and (iii) a subsequent reduction in seed production due to trade-offs in resource allocation. To strengthen the analyses of trade-offs, we test the assumption that total resource investment in seeds is constant across populations and is unrelated to seed traits.

MATERIAL AND METHODS

Study species and populations

Plantago coronopus L. ssp. *coronopus* (Plantaginaceae) is a widespread, short-lived perennial herb distributed along the Mediterranean basin, reaching northern Europe through a narrow strip along the Atlantic coast (Fig. 1; Hultén & Fries 1986). The subspecies *coronopus* is present throughout most of the species' range and differs from other less common subspecies in morphology of the bracts (Chater & Cartier 1976). Our study was restricted to the common subspecies, and hereafter we will be referred to as *P. coronopus*. It presents high variability in morphological characters and a life cycle that can be annual or perennial (Chater & Cartier 1976). Reproductive individuals have several spikes of wind-pollinated flowers and present intermediate outcrossing rates, with high variation among and within populations (Wolff *et al.* 1988). Fruits are capsules that produce two types of seed (Dowling 1933; Schat 1981): up to four large basal seeds and one or no small apical seeds (Fig. 2). Basal seeds further differentiate from apical seeds by the possession of a coat that becomes mucilaginous when moistened,

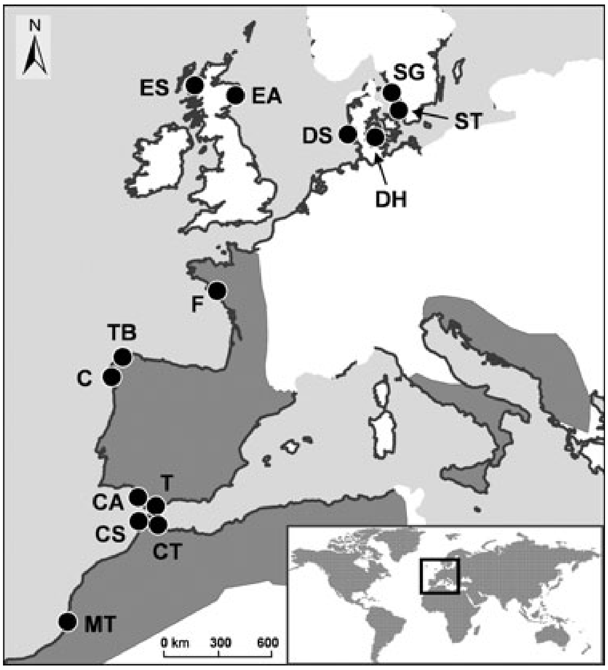

Fig. 1. Location of populations of *Plantago coronopus* sampled in the study (black dots). The distribution range of the species, according to Hultén & Fries (1986), is highlighted in grey (including coastal outlines). See Table 1 for population acronyms.

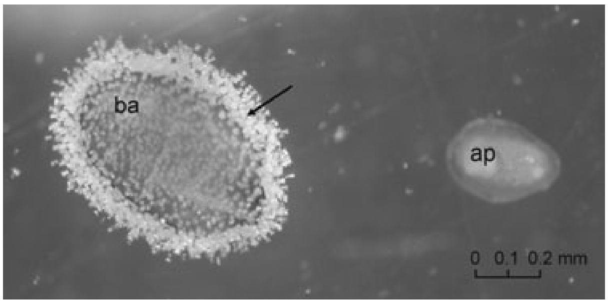

Fig. 2. Seed dimorphism in *Plantago coronopus*. A basal (ba) and an apical (ap) seed after 1 h soaked in water. Basal seeds are larger than apical seeds and possess a coat that becomes mucilaginous when moistened, as indicated by the arrow.

which is virtually absent in the latter seed type. *P. coronopus* is a coloniser plant occurring in many habitats, especially sand dunes, salt marshes, coastal prairies and human-disturbed environments.

In this study, we analysed 14 perennial populations, spanning almost the entire latitudinal range of the species along the eastern Atlantic coast (Table 1, Fig. 1): two populations in Morocco (Tiznit and Cap Spartel), five in Spain (Ceuta, Tarifa, Camposoto, Corrubedo and Traba), one in NW France (Pen Bron), two in Denmark (Helnaes and Skallingen), two in Sweden (Glommen and Torekov) and two in Scotland (Aberdeen and Skye). All populations were located by the sea, although the species' habitat on the seashore differed along the coast: populations in Tiznit (MT), Cap Spartel (CS) and Ceuta (CT) were located on coastal cliffs; populations in Tarifa (T), Camposoto (CA), Corrubedo (C), Traba (TB) and Pen Bron (F) were situated on sand dunes; and populations in Helnaes (DH), Skallingen (DS), Glommen (SG), Torekov (ST), Aberdeen (EA) and Skye (ES) were located on coastal prairies.

Environmental data

To estimate soil fertility in populations, we collected 10-cm deep soil cores and measured in the laboratory the percentage soil organic matter content from the organic carbon (Heanes 1984). Meteorological data were obtained from several databases: http://www.allmetsat.com (MT); *Direction Regional d'Hydraulique* in Tetuan, Morocco (CS); Spanish National Meteorological Agency (CT, T and CA); MeteoGalicia (C and TB); MeteoFrance (F); Danish Meteorological Institute (DH and DS); Swedish Meteorological and Hydrological Institute (SG and ST); and the Met Office (EA and ES). We obtained mean monthly precipitation (mm), mean monthly maximum and minimum temperatures (°C) and mean annual temperature (°C) for 10–20 years within the last four decades (depending on availability) from the nearest meteorological station to each population. We calculated total precipitation in the period of the growing season where highest differences appeared among populations, *i.e.* from June to September (thereafter 'summer precipitation'). We also calculated evapotranspiration (mm) using the equation (from Hargreaves 1985):

$$\mathrm{ET} = 0.00023 \cdot R_a \mathrm{TD}^{0.5}(\mathrm{T}_m + 1708) \cdot d$$

where ET is monthly evapotranspiration, R_a is extraterrestrial radiation (calculated as a function of latitude and month of the year; Allen *et al.* 1998), TD is the difference between mean

Table 1. Location of *Plantago coronopus* populations in the study and mean values in environmental variables: annual temperature, summer precipitation (P_S), summer water stress index (WSI_S; see Material and Methods for details) and percentage soil organic matter (SOM).

population	location	coordinates	temperature (°C)	P_s (mm)	WSI_s	SOM (%)
MT	Tiznit, Morocco	29°45′ N, 09°53′ W	18.5	5	99.0	–
CS	Cap Spartel, Morocco	35°47′ N, 05°55′ W	17.7	28	19.2	–
CT	Ceuta, Spain	35°54′ N, 05°21′ W	16.1	15	33.2	–
T	Tarifa, Spain	36°02′ N, 05°38′ W	17.1	31	11.7	0.7
CA	Camposoto, Spain	36°25′ N, 06°13′ W	18.7	38	11.4	0.4
C	Corrubedo, Spain	42°33′ N, 09°01′ W	14.9	166	2.6	1.1
TB	Traba, Spain	43°11′ N, 09°03′ W	14.7	198	2.2	1.4
F	Pen Bron, France	47°18′ N, 02°30′ W	12.8	150	2.6	0.9
DH	Helnaes, Denmark	55°08′ N, 09°59′ E	8.1	191	2.1	5.6
DS	Skallingen, Denmark	55°29′ N, 08°15′ E	9.1	313	1.2	17.9
SG	Glommen, Sweden	56°55′ N, 12°21′ E	8.0	327	1.1	0.8
ST	Torekov, Sweden	56°23′ N, 12°38′ E	8.8	286	1.3	6.1
EA	Aberdeen, Scotland	57°20′ N, 01°55′ W	8.6	250	1.3	18.1
ES	Skye, Scotland	57°30′ N, 06°26′ W	9.1	489	0.7	17.7

monthly maximum and minimum temperatures, T_m is the average monthly temperature, and d is the number of days in each month. For each population, we summed ET from June to September to calculate summer ET, and then calculated an index of summer water stress as the ratio between summer ET and summer precipitation.

Seed collection and measurements

We collected the spikes of 25 randomly chosen individuals in each population in the summers of 2007 or 2008. Fruits were dissected in the laboratory to measure a set of seed-related traits (Table 2). For five populations (MT, CS, CT, EA and ES) some variables were not calculated (Fig. 3). The number of basal and apical seeds per fruit was counted with magnifying glasses in 10 fruits per mother plant. The number of each type of seed per fruit and the total number of seeds per fruit (basal plus apical seeds; thereafter 'fruit seed production') was then averaged across individuals for each population. We also averaged across individuals the percentage of basal and apical seeds, and calculated the seed ratio from mean population values, dividing percentage of basal seeds by percentage of apical seeds (thereafter 'seed ratio'). As seed ratio increases, so does the predominance of basal seeds and thus the homogeneity in seed type.

Basal and apical seed mass was estimated for each population by weighing eight groups of 25 basal seeds and 25 apical seeds from 12 individuals (seeds were weighed in groups due to their small size). The mucilaginous coat was measured with the aid of magnifying glasses in five basal seeds per plant, with 15 plants per population. We first soaked the seeds for 1 h in Petri dishes until the mucilage became conspicuous (Fig. 2). We estimated the projected seed area and the total area that contained both the seed and the mucilaginous coat using the ellipse formula (area = $\pi \cdot a \cdot b$; a and b correspond to the major and minor semi-axes), and calculated the mucilage area by subtracting the seed area from the total area. For each population, we averaged across seeds the percentage areas of mucilage and seed, and then calculated from mean population percentages the ratio between mucilage and seed area (thereafter 'mucilage ratio'). We used a relative measure of mucilage because, in a linear regression (*lm* procedure, package *stats*; R Development Core Team 2011), mucilage area was positively correlated to seed area ($t_{857} = 22.6$, $R^2 = 0.37$, $P < 0.001$).

We estimated the total number of seeds per year (thereafter 'annual seed production') and the size of an average of 160 reproductive individuals per population and year in annual censuses from 2007 to 2010. Each year, we recorded the number of leaves and inflorescences of individuals, and the length of an average leaf and an average inflorescence. Plant size was defined as number of leaves*length of an average leaf, and annual seed production was estimated as number of inflorescences*length of an average inflorescence*number of seeds per unit of inflorescence length (calculated with a regression equation for each population). We also calculated the total seed production over the lifespan (thereafter 'lifetime seed production') for those reproductive individuals that were monitored for their entire lives. For further details on the estimation of these parameters, see Villellas *et al.* (2012). Annual seed production, lifetime seed production and plant size were then averaged for each population across individuals and years.

Finally, we estimated for each population the total mass allocation to seeds per fruit, per plant per year and per plant over the lifespan (thereafter 'fruit seed mass', 'annual seed mass' and 'lifetime seed mass', respectively) from mean values of the above parameters: fruit seed mass = (number of basal seeds per fruit*basal seed mass) + (number of apical seeds per fruit*apical seed mass); annual seed mass = annual seed production*(fruit seed mass/fruit seed production); lifetime seed mass = lifetime seed production*(fruit seed mass/fruit seed production).

Analysis of seed trait variability, environmental factors and plant size

We analysed among-population variability in seed traits with the coefficient of variation (CV) of population mean values. Since most of the traits were log-normally distributed, we also

Table 2. Description of seed traits measured in *Plantago coronopus,* and their variability among populations, estimated with the standard coefficient of variation (CV) of population mean values, and the coefficient of variation for log-normal distributions (CV_{ln}; see Material and Methods for details).

seed trait	description	CV	CV_{ln}
lifetime seed production	Total number of seeds per plant over the lifespan	0.74	0.77
annual seed production	Total number of seeds per plant per year	0.84	1.17
fruit seed production	Total number of seeds per fruit (basal plus apical seeds)	0.24	0.25
lifetime seed mass	Total mass of seeds per plant over the lifespan	1.12	1.20
annual seed mass	Total mass of seeds per plant per year	1.05	1.64
fruit seed mass	Total mass of seeds per fruit (basal plus apical seeds)	0.18	0.17
seed ratio	Ratio between basal and apical seeds	0.74	0.57
basal seed mass	Mass of basal seeds	0.31	0.31
apical seed mass	Mass of apical seeds	0.23	0.27
mucilage ratio	Amount of mucilage in basal seeds, relative to seed size	0.23	0.22

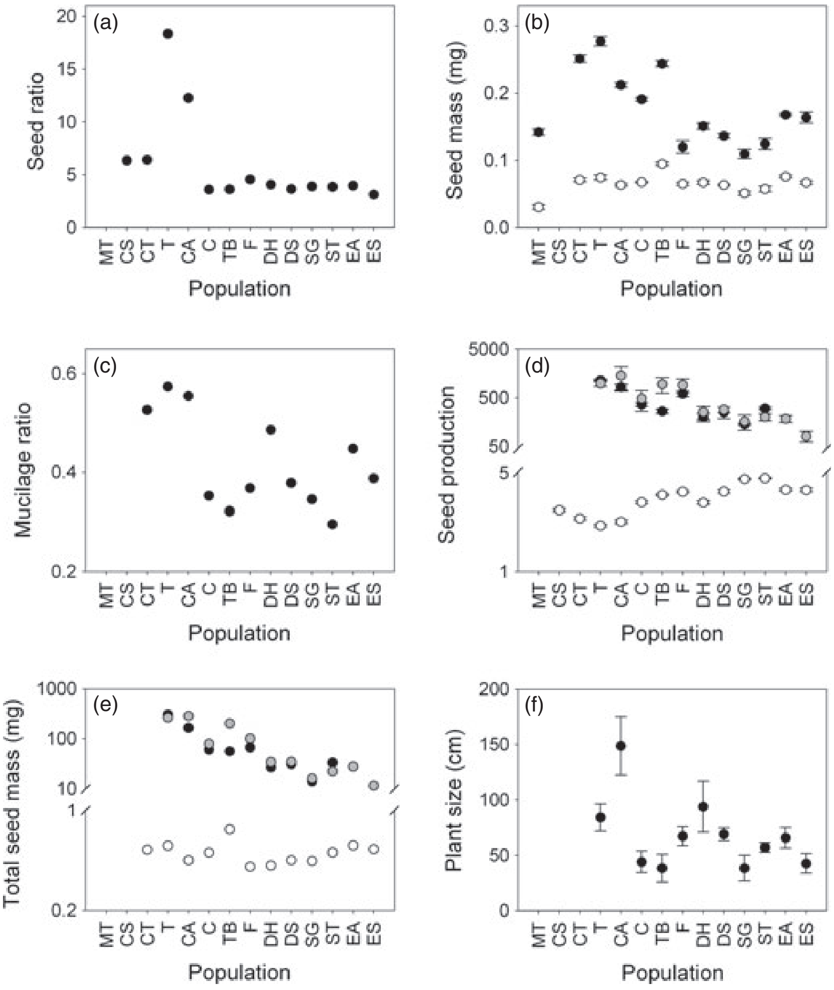

Fig. 3. Population averages (± SE in b, d and f) of seed traits in sampled populations of *Plantago coronopus*: (a) seed ratio; (b) basal seed mass (black) and apical seed mass (white); (c) mucilage ratio, (d) lifetime seed production (black), annual seed production (grey) and fruit seed production (white); (e) lifetime seed mass (black), annual seed mass (grey) and fruit seed mass (white); and (f) plant size. Populations are ranked from left to right by increasing latitude. Note logarithmic scale and a break in vertical axis in (d) and (e). For five populations (MT, CS, CT, EA and ES) some variables were not calculated.

calculated the coefficient of variation appropriate for this distribution, as $\mathrm{CV_{ln}} = \sqrt{e^{(s^2)} - 1}$, where e is the base of the natural logarithm and s is the standard deviation of the natural-log transformed data (Koopmans *et al.* 1964).

The effects of environmental factors on seed trait variation were tested on those traits conferring stress tolerance to plants, *i.e.* seed mass and mucilage (see Introduction; thereafter 'stress tolerance traits'). Considering the particular dimorphism of the species, in which basal seeds are larger than apical seeds and the latter lack the mucilaginous coat, we selected the following stress tolerance traits: seed ratio, basal seed mass and mucilage ratio (all of them log-transformed). We analysed collinearity among environmental variables with an analysis of variance inflation factor (*vif* procedure, package *car* in R), and discarded summer water stress index from subsequent analyses because it showed high collinearity with summer precipitation (values much higher than 10; Kleinbaum *et al.* 1988) and because the latter provided a better fit to our data. Thus, the environmental predictors were mean annual temperature, summer precipitation (log-transformed) and soil fertility (log-transformed). For each stress tolerance trait, we performed linear regressions with each of the three predictors, as well as multiple linear regressions with all possible combinations with two or three predictors (*lm* procedure, package *stats* in R). To find which model provided the best fit to our data, we first compared the AIC (Akaike information criterion) values from all regression analyses. Among the combinations of predictors with the lowest AIC values, we then checked with ANOVA if the sequential addition of predictors significantly improved the previous simpler model (ANOVA procedure, package *stats* in R). For these analyses, we used the populations for which we had data for all environmental predictors and stress tolerance traits (all except MT, CS and CT), so that AIC values were comparable.

We also analysed whether plant size (log-transformed) was correlated with seed-related traits using linear regressions, although the effect of plant size on lifetime and annual seed production was instead analysed with linear mixed models, including population and year as random factors (*lme* procedure, package *nlme* in R).

Analysis of the tolerance–fecundity trade-off

To test for a trade-off between fecundity and stress tolerance, we used estimates of seed production at three levels: lifetime seed production, annual seed production and fruit seed production. First, we performed simple linear regressions between each measure of seed production (response variables) and each stress tolerance trait (predictors), with log-transformed variables except for fruit seed production. Then we tested again the relationship between each seed production trait and each stress tolerance trait with multiple regressions, including plant size as a covariate to control for its possible effects, and examining significance of the partial regression parameters of stress tolerance traits. Finally, to check for the assumption of constant available resources for seeds in the tolerance–fecundity trade-off, we performed Pearson's correlation analyses between lifetime, annual and fruit seed mass on the one hand, and seed production traits and stress tolerance traits on the other hand (*cor* procedure, package *stats* in R).

The tolerance–fecundity trade-off was tested for each fecundity level using three stress tolerance traits, which may increase the probability of type I error. For all the analyses, we thus performed at each fecundity level corrections on *P*-values with the false discovery rate method (Benjamini & Hochberg 1995), appropriate for analyses with small sample sizes.

RESULTS

Seed trait variability

Seed traits exhibited large differences in among-population variability (Table 2): lifetime and annual seed mass, lifetime and annual seed production, and seed ratio showed the highest variability, whereas fruit seed mass was the least variable trait. Apical seed mass was less variable across the study area than basal seed mass. Both measures of variability among populations (CV and CV_{ln}) showed the same pattern across traits.

Effects of environmental factors and plant size

There were notable differences among populations in temperature, summer precipitation and soil fertility along the latitudinal gradient (Table 1). There was a gradual increase in temperature from north to south, and northern populations generally had higher precipitation, with a few exceptions in both climate parameters. Southern populations in Spain and France had lower soil fertility than most northern populations.

Stress tolerance traits were significantly correlated to environmental predictors, although in different ways (Table 3). The separate effect of summer precipitation was more significant than that of temperature or soil fertility on seed ratio and mucilage ratio, whereas temperature showed the highest separate effect on basal seed mass. In the case of seed ratio, the combination of summer precipitation and temperature had the lowest AIC value, but the ANOVA indicated that it did not explain differences among populations significantly better than summer precipitation alone. For basal seed mass, temperature and soil fertility together had the lowest AIC value, and provided a better fit to the data than temperature alone, although with marginal significance. In the case of the mucilage ratio, the combination of the three predictors had the lowest AIC value, but it did not improve a model with summer precipitation and soil fertility. However, the combination of summer precipitation and soil fertility explained differences in mucilage ratio better than summer precipitation alone, although with marginal significance. Summer precipitation negatively affected seed ratio and mucilage ratio, but had no effect on basal seed mass. Temperature positively affected all stress tolerance traits, and the effect of soil fertility was always negative.

Plant size was significantly and positively correlated with lifetime seed production ($F_{1,2618} = 858.4$, $P < 0.001$), annual seed production ($F_{1,5286} = 2317.3$, $P < 0.001$), seed ratio ($F_{1,9} = 7.6$, $R^2 = 0.46$, $P = 0.022$) and mucilage ratio ($F_{1,9} = 14.9$, $R^2 = 0.62$, $P = 0.004$), and significantly and negatively correlated with fruit seed production ($F_{1,9} = 6.6$, $R^2 = 0.42$, $P = 0.030$). In contrast, plant size had no significant effect on lifetime seed mass ($F_{1,7} = 2.7$, $R^2 = 0.28$, $P = 0.144$), annual seed mass ($F_{1,9} = 2.3$, $R^2 = 0.21$, $P = 0.162$), fruit seed mass ($F_{1,9} = 2.0$, $R^2 = 0.18$, $P = 0.188$), basal seed mass ($F_{1,9} = 0.5$, $R^2 = 0.05$, $P = 0.514$) and apical seed mass ($F_{1,9} = 0.1$, $R^2 = 0.02$, $P = 0.713$). In some of these regressions, however, Cook's distance for population TB was larger than $4/n$ (where n is number of observations in the regression), which might be problematic (Bollen & Jackman 1990). TB showed, compared to other populations, high or intermediate levels of seed production and total seed mass per individual, despite having small plant sizes (Fig. 3). We thus repeated analyses of the effects of plant size without data from TB: the significance of correlations were not affected, except between plant size and annual seed mass, which became significant and positive ($F_{1,8} = 7.5$, $R^2 = 0.48$, $P = 0.025$). The correlation between plant size and lifetime seed mass was also higher without TB, but not significant ($F_{1,6} = 3.2$, $R^2 = 0.35$, $P = 0.122$).

Tolerance–fecundity trade-off

Southern populations showed, in general, higher seed ratios, higher basal seed mass and higher mucilage ratio than northern populations, whereas apical seed mass presented low variation along the latitudinal gradient (Fig. 3a–c). Southern populations

Table 3. Results from regression analyses between environmental predictors (P_S: summer precipitation; Te : mean annual temperature; SOM : soil organic matter) and stress tolerance traits in *Plantago coronopus.* AIC values correspond to Akaike information criterion (only the three combinations of predictors with the lowest AIC values are shown). Model comparisons, performed with ANOVA, show whether the sequential addition of predictors significantly improves the previous simpler model. The combination of predictors that constituted the best model for each stress tolerance trait is highlighted in bold. *F* statistics are subindexed with corresponding degrees of freedom.

stress tolerance traits	predictors	effects of environmental gradient				model comparison	
		F	R^2	P	AIC	F	P
seed ratio	**P_s**	$76.5_{1,9}$	0.89	<0.001	−19.3	–	–
	P_s and Te	$45.9_{2,8}$	0.92	<0.001	−20.2	$2.5_{1,8}$	0.152
	P_s and Te and SOM	$27.6_{3,7}$	0.92	<0.001	−18.6	$0.2_{1,7}$	0.664
basal seed mass	Te	$12.0_{1,9}$	0.57	0.007	−18.0	–	–
	Te and **SOM**	$9.8_{2,8}$	0.71	0.007	−20.3	$3.8_{1,8}$	0.086
	Te and SOM and P_S	$5.9_{3,7}$	0.72	0.024	−18.6	$0.2_{1,7}$	0.674
mucilage ratio	P_s	$10.2_{1,9}$	0.53	0.011	−24.0	–	–
	P_s and **SOM**	$9.8_{2,8}$	0.71	0.007	−27.4	$5.0_{1,8}$	0.056
	P_S and SOM and Te	$7.5_{3,7}$	0.76	0.013	−27.5	$1.5_{1,7}$	0.255

generally had lower fruit seed production than northern populations, but higher lifetime and annual seed production (Fig. 3d).

Simple regression analyses showed that lifetime seed production was positively and significantly correlated with seed ratio, and marginally significantly correlated with basal seed mass and mucilage ratio, whereas in multiple regression analyses including plant size as a covariate, the partial correlations were not significant for any stress tolerance trait (Fig. 4a–c, Table 4). Annual seed production was positively correlated with seed ratio, with marginal significance, and not significantly correlated with basal seed mass and mucilage ratio, while none of their partial correlations were significant in regression analyses including plant size (Fig. 4d–f, Table 4). Fruit seed production was significantly and negatively correlated with seed ratio, basal seed mass and mucilage ratio (Fig. 4g–i, Table 4); when accounting for plant size, the partial correlation was still significant and negative for basal seed mass, and marginally significant for seed ratio and mucilage ratio.

Lifetime seed mass was significantly correlated with lifetime seed production ($t_7 = 9.1$, $r = 0.96$, $P < 0.001$), seed ratio ($t_7 = 4.4$, $r = 0.86$, $P = 0.009$) and basal seed mass ($t_7 = 3.4$, $r = 0.79$, $P = 0.018$), and correlation with mucilage ratio was marginally significant ($t_7 = 2.3$, $r = 0.65$, $P = 0.056$). Annual seed mass was significantly correlated with annual seed production ($t_9 = 13.5$, $r = 0.98$, $P < 0.001$), seed ratio ($t_9 = 3.0$, $r = 0.71$, $P = 0.023$) and basal seed mass ($t_9 = 3.2$, $r = 0.73$, $P = 0.023$), although it showed no correlation with mucilage ratio ($t_9 = 1.4$, $r = 0.44$, $P = 0.181$). Fruit seed mass showed no significant correlation with fruit seed production ($t_{10} = -0.3$, $r = -0.09$, $P = 0.783$), seed ratio ($t_{10} = 0.1$, $r = 0.01$, $P = 0.977$) or mucilage ratio ($t_{10} = -0.4$, $r = -0.12$, $P = 0.977$), and showed a marginally significant correlation with basal seed mass ($t_{10} = 2.6$, $r = 0.64$, $P = 0.076$). Lifetime and annual seed mass decreased northwards, whereas fruit seed mass showed no clear latitudinal pattern (Fig. 3e).

DISCUSSION

Plantago coronopus presents considerable variation along the Atlantic coast in Europe and North Africa in a set of seed traits, *i.e.* the number and size of seeds, the proportion of basal and apical seeds and the production of mucilage. Similar levels of variability have been found among populations of other

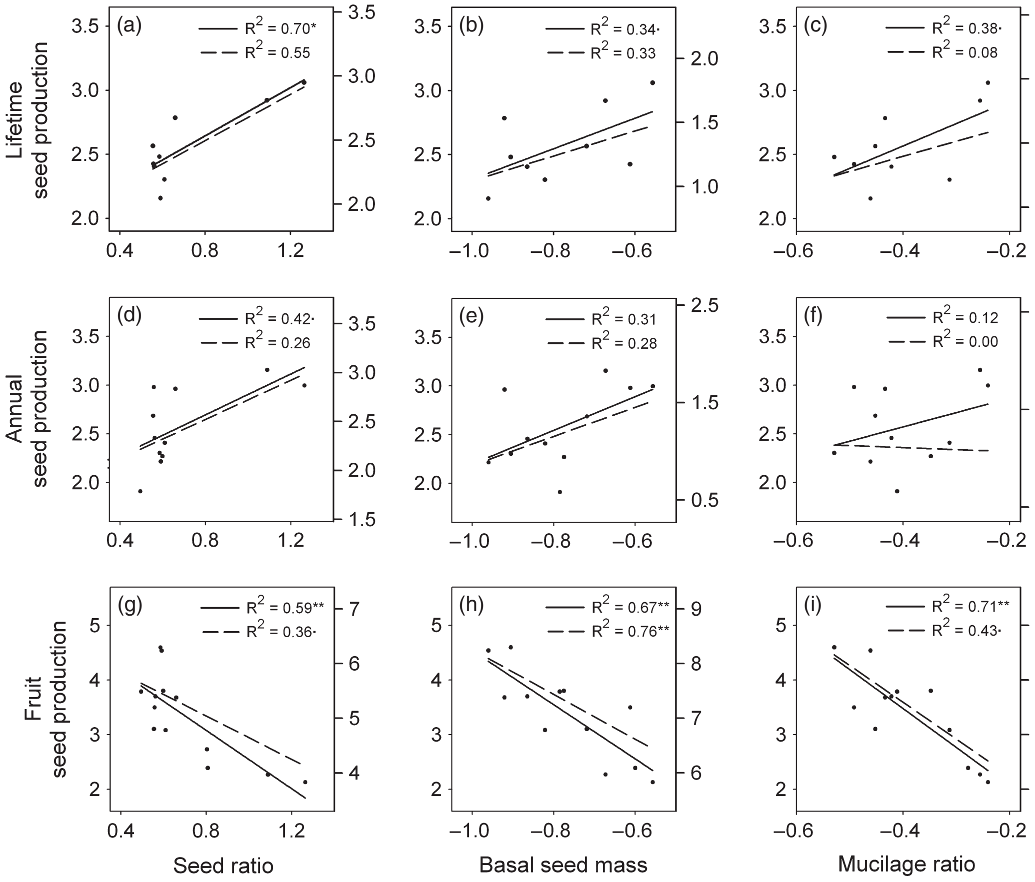

Fig. 4. a–i: Relationship between lifetime, annual and fruit seed production, on the one hand, and stress tolerance traits (seed ratio, basal seed mass and mucilage ratio), on the other, in *Plantago coronopus*. Continuous lines represent linear regressions between seed production traits and stress tolerance traits (left vertical axis), dashed lines represent partial regressions between seed production traits and stress tolerance traits after controlling for plant size (right vertical axis). All variables were log-transformed except for fruit seed production. Note small differences in scale among seed production traits and among stress tolerance traits. R^2 coefficients are accompanied by statistical significance: $\cdot P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; *P*-values were corrected by the false discovery rate method.

Table 4. Tolerance-fecundity trade-off: regression analyses between fecundity traits (lifetime, annual and fruit seed production) and stress tolerance traits. In multiple regression analyses, plant size is included as a covariate and partial regression estimates (β) are shown. F statistics are subindexed with corresponding degrees of freedom, and *P*-values are corrected by the false discovery rate method.

					multiple regression					
		simple regression			stress tolerance trait			plant size		
fecundity traits	stress tolerance traits	F	R^2	*P*	β	t	*P*	β	t	*P*
lifetime	Seed ratio	$16.6_{1,7}$	0.70	0.014	0.90	2.7	0.104	0.08	0.2	0.865
	Basal seed mass	$3.6_{1,7}$	0.34	0.099	0.97	1.7	0.210	0.72	1.7	0.423
	Mucilage ratio	$4.2_{1,7}$	0.38	0.099	1.18	0.7	0.486	0.37	0.4	0.865
annual	Seed ratio	$6.4_{1,9}$	0.42	0.096	1.00	1.7	0.197	0.09	0.1	0.910
	Basal seed mass	$4.1_{1,9}$	0.31	0.109	1.49	1.8	0.197	0.78	1.3	0.537
	Mucilage ratio	$1.2_{1,9}$	0.12	0.298	−0.21	−0.1	0.927	1.1	1.0	0.537
fruit	Seed ratio	$15.9_{1,11}$	0.59	0.002	−1.97	−2.1	0.066	−1.00	−0.8	0.675
	Basal seed mass	$20.4_{1,10}$	0.67	0.002	−4.10	−5.0	0.003	−2.16	−3.7	0.018
	Mucilage ratio	$24.7_{1,10}$	0.71	0.002	−6.76	−2.5	0.059	−0.05	−0.4	0.971

widespread plants in some seed traits. For example, the CV for seed size similarly lies around 0.20–0.30 in the short-lived *Campanula americana* (calculated from Kalisz & Wardle 1994) and the long-lived *Vaccinium stamineum* (Yakimowski & Eckert 2007), and the CV for annual reproductive output (number of seeds or fruits per plant per year) in those species is also more than 0.70. In this study, we tested whether the observed intraspecific variability was explained by a recent hypothesis proposed at the community level: the trade-off between stress tolerance and fecundity in heterogeneous environments (Muller-Landau 2010). Our results suggest indeed that a tolerance–fecundity trade-off at the fruit level underpins, to a certain extent, variation in seed traits among populations of *P. coronopus*. However, seed production shows the opposite pattern at the individual and fruit level, which appears to be an additional strategy of the species to adapt to the stress gradient, as explained below.

Stress tolerance traits were strongly correlated with climatic and soil conditions in *P. coronopus*. Basal seed mass was, on the one hand, enhanced by temperature, which may have increased energy requirements of metabolic processes (Murray *et al.* 2004), and on the other hand, negatively affected by soil organic matter, which is associated with fertility (Reeves 1997). Furthermore, both temperature and soil organic matter may have also indirectly affected basal seed mass through their effects on water availability (Cobertera 1993). Mucilage ratio was in turn negatively affected by summer precipitation and soil organic matter, both associated with moisture, suggesting a role of mucilage in reducing water deficit. Finally, seed ratio, which represents the relation between basal and apical seeds, and thus incorporates both the variation in seed mass and in mucilage, was negatively affected by summer precipitation. Overall, the environmental parameters analysed in this study represent some form of environmental stress (water and nutrient availability, energy requirements), and significantly contribute to explain among-population differences in one or more stress tolerance traits. Our results agree with previous studies that found tolerance-related seed traits, most commonly seed size, associated with higher temperatures (Baker 1972; Murray *et al.* 2004), lower precipitation or water availability in general (Baker 1972; Wright & Westoby 1999), and lower soil fertility (Lee & Fenner 1989; Parolin 2000). There is also abundant literature that relates seed size with seedling competitive ability (*e.g.*, Tilman 1994; Geritz *et al.* 1999), but this factor seems not to explain seed trait variation in *P. coronopus*, because the populations exposed to highest competition (in northern coastal meadows) had the smallest seeds.

The tolerance–fecundity model (Muller-Landau 2010) states that heterogeneous areas in terms of environmental stress provide different regeneration niches, allowing the maintenance of species with different seed sizes within communities, and assumes that seed size is related to stress tolerance. We believe that a similar mechanism underlies variability in seed traits at the fruit level among populations of *P. coronopus*, considering the large differences in climate and soil conditions among locations and the corresponding variation in seed traits. Let us consider the stress gradient that broadly coincides with the latitudinal gradient of the species, and along which fecundity (at the fruit level) and stress tolerance traits co-vary (Fig. 5). In this gradient, southern populations are subject to higher environmental

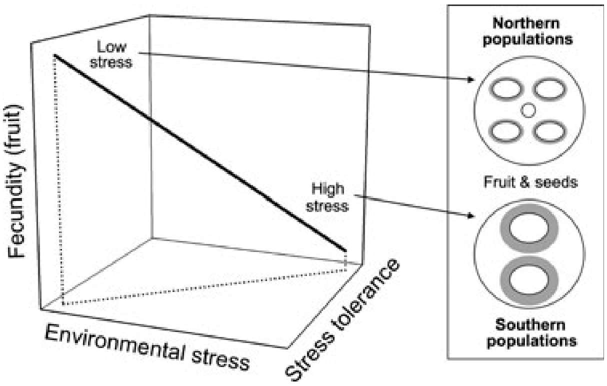

Fig. 5. Model showing a trade-off between fecundity (at the fruit level) and stress tolerance among populations of *Plantago coronopus* under a gradient of environmental stress. Diagram on the right represents differences in seed traits between the hypothetical extremes of the gradient (northern and southern populations). Basal seeds are surrounded with a mucilaginous coat (grey outline), which is absent in the smaller apical seeds. Note differences between fruits in size and mucilage production of basal seeds, and in the number of each seed morph.

stress (higher temperatures, lower summer precipitation, lower soil fertility) than northern populations, which limits their access to two essential resources for seed and seedling performance, *i.e.* water and nutrients. In response to these conditions, plants produce basal seeds with more internal resources to tolerate environmental stress (Chapin *et al.* 1993; Westoby *et al.* 2002; Coomes & Grubb 2003), and higher amounts of mucilage to facilitate water absorption (Harper & Benton 1986; Schat 1981; Gutterman & Shem-Tov 1997). For identical reasons, southern plants also increase the seed ratio, towards more basal relative to apical seeds. Since total resources allocated to seeds by fruits are constant across populations, the final outcome is a reduction in the total number of seeds per fruit, in consonance with the classical trade-off between seed size and seed number (Smith & Fretwell 1974; Lloyd 1988). Conversely, northern populations occur in less stressful conditions, and plants can thus reduce investment in seed size and mucilage, allowing an increase in fruit seed production (Fig. 5). A decline in seed size with latitude seems to be a common pattern within widespread plant taxa (Moles & Westoby 2003). In this model, *P. coronopus* adjusts the coexistence of basal and apical seeds along the stress gradient, resulting in a higher predominance of the more tolerant seed morph in populations under higher stress. This is equivalent to how big-seeded species would predominate over small-seeded species in stressful sites within communities. Overall, our results strongly suggest that the mechanism proposed by Muller-Landau (2010) for the maintenance of variation in seed size among species helps to explain the variability in seed traits among populations of *P. coronopus*.

The tolerance–fecundity trade-off operates in *P. coronopus* at the fruit level but not at the individual level, as indicated by the lack of negative correlations between lifetime and annual seed production and stress tolerance traits. Mendez (1997) also found in *Arum maculatum* a negative correlation between seed size and number only at the fruit level, whereas Devlin (1989) and Mehlman (1993) reported a trade-off at both levels in two perennial plants, which confirms the importance of considering different levels when analysing species seed production (Primack 1987; Herrera 1991). In *P. coronopus*, despite higher stress tolerance of seeds in southern populations, recruitment is still lower in these locations than in northern populations (Villellas *et al.* 2012), highlighting the stressful conditions for germination and/or early survival of plants in sand dunes. Thus, the higher seed production at the individual level in southern populations would constitute an additional strategy to compensate for a failure in recruitment (Villellas *et al.* 2012; see other compensatory changes in vital rates in Doak & Morris 2010), and would explain the opposite pattern between fruit seed production and lifetime and annual seed production. Such an increase in seed production per plant would be achieved through a larger number of fruits rather than a larger number of seeds per fruit. The production of many fruits with few seeds per fruit in the rather unpredictable environments of southern locations, moreover, can be seen as a way of bet-hedging, spreading the risk of failure in recruitment in space or time (Cohen 1966). In contrast with southern populations, the higher recruitment in northern populations, located in more humid and stable habitats, makes it unnecessary to put extra investment into total seed production, other than increasing seed number at the fruit level.

The compensatory increase in seed production per plant in southern populations, made possible by higher resource availability for reproduction per individual, seems in part achieved through larger plant sizes, as shown by the positive correlations between plant size, annual seed mass and annual seed production (see also Braza *et al.* 2010; Villellas *et al.* 2012). Such an increase in total seed production through larger plant sizes seems to be a common phenomenon for large-seeded relative to small-seeded species (Moles *et al.* 2004; Aarssen 2005). However, the process is less clear in *P. coronopus* over the lifespan of the plants, as plant size was correlated with lifetime seed production but not significantly with lifetime seed mass. Since there are no differences between individuals of southern and northern populations in the number of reproductive years (Villellas *et al.* 2012), such a lack of clear patterns over the lifespan might reflect our inability to detect the effects due to a low sample size (there is actually a tendency for a correlation), or to additional unknown factors. Nevertheless, the absence of trade-offs in resource allocation at the individual level responds to a latitudinal co-variation of annual and lifetime seed mass with some stress tolerance traits and seed production traits, in contrast to the relative constancy of fruit seed mass across the species range.

Population TB seems to be an outlier in the relationship between plant size and seed production traits, having smaller plants than expected and/or higher seed production and total seed mass at the individual level. The smaller plant sizes in TB are likely due to local periodic flooding with seawater (J. Villellas, personal observation), as submergence is expected to reduce plant growth (Schat 1984; Mommer & Visser 2005). The relatively high reproductive allocation per individual is more difficult to interpret, although Waite & Hutchings (1982) obtained similar results in coastal populations of the same taxon in England at different levels of exposure to seawater flooding. It could be that the resources not used for plant growth during such floods were allocated to reproduction in the longer periods of emergence.

To conclude, the large variation in seed traits and seed production among populations of the widespread *P. coronopus* seems to be explained by a combination of different processes, depending on the level of study. At the fruit level, the trade-off between seed production and stress tolerance seems to play a central role in maintaining variability among populations in traits such as seed size, mucilage production and the relative abundance of seed morphs. The tolerance–fecundity model may indeed help to understand why the production of different seed morphs with contrasting tolerance attributes, common in plants of stressful and unpredictable environments (Venable 1985; Imbert 2002), might vary among populations. For example, Ungar (1987) reported for the widespread dimorphic *Atriplex triangularis* a higher proportion of the tolerant seed morph, accompanied by a reduction in seed production per plant in populations subject to the highest salinity stress, and Yao *et al.* (2010) proposed a similar model for *Chenopodium album*. From a broader perspective, the tolerance–fecundity hypothesis might constitute a more general framework than the classical compromise between seed size and number, at least for species occurring along gradients in environmental stress. Rather than focusing only on seed size, we would expect any additional investment in seed tolerance in response to stress, such as mucilage, to trade-off against fecundity, thus promoting variability among populations. However, despite the generality of model, the results found for *P. coronopus* at the individual level indicate that additional factors, such as plant size or total resource availability, should be considered when analysing seed traits and reproductive allocation under stress gradients. Comprehensive studies that include the relevant stress tolerance traits and consider different fecundity levels will allow us to understand the diverse strategies of widespread plants to maximise fitness in each set of local conditions.

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Chapter 4

Environmental, genetic and geographical correlates of phenotypic variation within populations of a common herb in Europe

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Ecosphere (*in review*)

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Analyzing the patterns and causes of phenotypic and genetic variation within populations might help to understand life-history variability in plants, and to predict their responses to changing environmental conditions. Here we compare phenotypic variation and genetic diversity of the widespread herb Plantago coronopus across Europe, and evaluate their relationship with environmental and geographical factors. Genetic diversity was estimated in 18 populations from molecular markers with AFLP, and phenotypic variation was measured in a subset of 11 populations on six ecologically relevant traits (plant size, plant growth, fecundity, seed mass, mucilage production and ratio between two seed morphs). We also estimated variability in local environmental factors such as temperature, precipitation and intraspecific competition, and accounted for the central vs. peripheral position of populations. Phenotypic variation and genetic diversity and were not significantly correlated within populations throughout the species' range. Phenotypic variation was positively linked to precipitation variability, whereas genetic diversity was correlated with the position of populations, which suggests that both types of variation are shaped by different processes. Precipitation regime seems to have acted as a selective agent for variation within populations in most life-history traits, whereas the species' demographic history has probably reduced genetic diversity in northern peripheral populations with respect to central ones. The positive association found between precipitation variability and phenotypic variation also suggests that plant populations may have a higher adaptive potential in variable rather than stable environments. Our study offers an additional criterion when predicting the future distribution of species under environmental changes.

Key words: Adaptive variation, environmental fluctuations, Europe, evolutionary potential, genetic diversity, latitudinal gradient, marginal populations, phenotype, *Plantago coronopus*, precipitation, widespread short-lived perennial.

Introduction

The variation in life-history traits shown by plant populations constitute the basis for the evolutionary potential of species (Bradshaw 1991, Bradshaw and McNeilly 1991), and might have a critical role in the face of changing environmental conditions (Reed and Frankham 2001, Dawson et al. 2011). Numerous studies have reported indeed important effects of climate change on the ecology of plant and animal taxa (e.g., Walther et al. 2005, Parmesan 2006), and the existence of a pool of individuals potentially pre-adapted to different environmental scenarios may be important in the near future (Volis et al. 1998, Jump and Peñuelas 2005). Thus, analyzing intraspecific variation in life-history traits and its underlying causes will help to understand the adaptation mechanisms of plants to their current environment, and predict with more precision their future performance in new ecological scenarios.

Intuitively, phenotypic variation should show a correlation with genetic variation. However, genetic diversity based on molecular markers, which has been indeed used to assess the status and evolutionary potential of populations (*e.g.*, Frankham 1995, Haig 1998), has shown no consistent relationship with phenotypic variability (Butlin and Tregenza 1998, Reed and Frankham 2001). In fact, both metrics seem to be affected by different processes. Genetic diversity is usually inferred from neutral loci (Lynch et al. 1999, Holderegger et al. 2006). Thus, it will be mainly affected by the demographic history of species, through processes such as gene flow, genetic drift and founder events (Knapp and Rice 1998, Holderegger et al. 2006, Mitchell-Olds and Schmitt 2006, Lawton-Rauh 2008). For this reason, we could expect neutral genetic diversity to be correlated with the relative position of populations within species' ranges: peripheral populations will theoretically present lower genetic variation than central ones, because gene flow and population sizes typically decrease towards range edges, and bottlenecks and founder events are thus more likely (Lesica and Allendorf 1995, Vucetich and Waite 2003). In contrast, phenotypic variation is frequently estimated on fitness-related characters, which are likely to be affected by the process of natural selection. Therefore, genetic diversity inferred from marker loci does not necessarily constitute the best predictor for variation in life-history traits (Reed and Frankham 2001).

Phenotypic variation within populations may instead show a closer relationship with environmental conditions. Climate, for example, is a major selective agent in plants at large spatial scales (Weber and Schmid 1998, Joshi et al. 2001, Etterson 2004), and variability in life-history traits could be promoted through natural selection by variation in factors such as temperature and precipitation. Environmental variability might also trigger trait variation by means of phenotypic plasticity, which has indeed a genetic basis as well (Schlichting 1986, Thompson 1991, Pigliucci 2005). Thus, phenotypic variation within populations is expected to show a positive correlation with variation in environmental conditions both through adaptive genetic variation and plasticity. Adaptive traits may also present the signal of neutral processes such as gene flow or founder events (van Tienderen et al. 2002), but to a lesser extent (Galloway and Fenster 2000, Joshi et al. 2001). Thus, the effects of local environmental variability and the spatial position of populations should be examined together throughout a species' distribution range, on both the genetic and phenotypic variation within populations. In this way, we can contribute to unravel the consequences of the adaptive selection and demographic history of species.

Widespread plants represent successful examples of life history adaptability to a broad range of local conditions (Baker 1974, Waldmann and Andersson 1998, Joshi et al. 2001) and provide a good opportunity to analyze phenotypic variation along large geographical and/or environmental gradients. For this reason we chose as our study case *Plantago coronopus*, a widespread short-lived herb in Europe, N Africa and SW Asia (Hultén and Fries 1986). This taxon presents high variability in vegetative and reproductive traits, as well as in demographic vital rates, both at regional (Waite and Hutchings 1982, Braza et al. 2010) and continental scales (Villellas et al. 2012, Villellas and García 2012, Villellas et al. *in press*). Furthermore, *P. coronopus* produces two types of seeds that differ in size and in the production of a mucilaginous coat that facilitates water absorption (Dowling 1933). Variation among populations of this taxon in traits such as plant size, seed size and mucilage production appears to be highly related to environmental factors such as precipitation, temperature and intraspecific competition (Villellas et al. 2012, Villellas and García 2012). However, it remains to be tested whether variability in environmental conditions promotes phenotypic variation within populations as well.

In this study we analyze both phenotypic variability and genetic diversity in the widespread *P. coronopus*. We sampled 18 populations spanning the whole latitudinal gradient of the species in Europe, for which we quantified genetic diversity by using amplified fragment length polymorphism (AFLP). Individual plants of a subset of 11 populations were intensively monitored in the field for a minimum of 4 yr, to calculate within-population variability in six key life-history traits that encompass different parts of the life cycle: plant size, annual plant growth, fecundity, seed mass, mucilage production, and ratio between seed morphs. Seed mass, ratio between seed morphs, and mucilage are of high ecological importance for plants (Harper and Benton 1966, Westoby et al. 1992, Imbert 2002, Villellas and García 2012), and growth and fecundity constitute key components of population dynamics for short-lived taxa like *P. coronopus* (Silvertown et al. 1996). The temporal variability in local climate and intraspecific competition was also estimated, and the central *vs*. peripheral position of populations was accounted for. We aimed to explore the pattern and causes of phenotypic and genetic variation within populations of a widespread plant in a large latitudinal gradient in Europe. Our goal was to disentangle the effects of adaptive variation in response to environmental conditions, from the influence of range position and the associated demographic history of populations.

Material and methods

Species and populations studied

Plantago coronopus L. (buck's horn plantain, Plantaginaceae) is a widespread short-lived herb, mainly distributed around the Mediterranean Basin, although it also reaches N Europe through a strip along the Atlantic coast (Hultén and Fries 1986, Fig. 1a). We have worked with the most common subspecies *Plantago coronopus* ssp. *coronopus*, which can be distinguished from the others by the morphology of the bracts (Chater and Cartier 1976). Hereafter we will refer to it as *P. coronopus*. Plants have one or a few rosettes, producing several spikes with wind-pollinated flowers. Each fruit produces two types of seeds in variable number: up to four large, basal seeds, and one or no small apical seeds. Basal and apical seeds further differentiate in the timing and percentage of germination (Braza and García 2011), and only the former possess a mucilaginous coat that facilitates water absorption (Dowling 1933). Thus, basal seeds seem to be better adapted for habitats with low water or resources supply. *P. coronopus* shows high variability among individuals in other characters such as leaf shape and size.

Plantago coronopus is present in a wide variety of environmental conditions across its range in terms of climate, soil richness and vegetation cover. In central areas, the species is found in coastal and inland locations, in contrasting habitats like sand dunes, cliffs, shrublands or human-disturbed areas. Northern peripheral populations, on the contrary, are rather restricted to coastal places (coast prairies, salt marshes). To analyze genetic diversity, we have chosen in this study 11 central and 7 northern peripheral populations, for a total of 18 populations in six countries, spanning the whole latitudinal and environmental gradient of the species in Europe (Fig. 1a, Table 1). Peripheral populations were located in coastal meadows, and central populations were located in a variety of habitats. For the analysis of phenotypic variability, we have used a representative subset of 5 central and 6 peripheral populations, for a total of 11 populations along the Atlantic coast (Fig. 1a, Table 1).

Variability in phenotypic traits

Eleven populations were monitored during up to 8 yr (between 2003 and 2010; Table 1) to quantify within-population variability in six life-history traits. With a several-year dataset for some traits, we can assure that our phenotypic measurements are representative of each population, and not influenced by the particular conditions of a given year. On each population, we labelled between 50 and 150 reproductive plants to measure each year the number and length of leaves, and the number and length of inflorescences. Plant size was estimated by multiplying the number of leaves and the length of an average leaf. Plant growth rate was calculated as the ratio between plant size in one year and that of the previous year. We estimated fecundity (number of seeds) from the number of inflorescences × length of an average inflorescence × number of seeds per unit of inflorescence length (calculated with a regression equation for each population). We found in a preliminary analysis that fecundity was correlated with plant size (log-transformed variables; $F_{1,7348} = 3754$, $R^2 = 0.34$, $p < 0.001$; *lm* procedure, package *stats*, R Development Core Team 2011), so we calculated fecundity per unit of plant size (hereafter "fecundity") and used it for subsequent analyses.

To evaluate variation in seed traits, the spikes of 25 individuals were collected on each population in the summers of 2007 or 2008. In the laboratory, we counted the total number of basal and apical seeds in 10 fruits per plant. We then calculated the ratio of basal and apical seeds for each individual (hereafter "seed ratio";

not available in population BN) by dividing the total number of basal seeds by that of apical seeds. The production of mucilage and the size of basal seeds were measured in five seeds per individual, in an average of 15 individuals per population. We first soaked the seeds for 1 h in Petri dishes, until mucilage became conspicuous. We then measured the projected seed area, and the total area that contained both the seed and the mucilaginous coat, using the ellipse area formula. Seed mass was estimated from seed area, and mucilage production (hereafter "mucilage ratio") was estimated by substracting the seed area from the total area, and by dividing the result by the seed area. We used a relative measure of mucilage because the area of the mucilaginous coat was positively correlated to seed mass (Villellas and García 2012). For seed mass and mucilage ratio, we calculated for each individual the average across seeds.

For each population, we estimated phenotypic variation from the coefficient of variation (CV) among individuals in each trait: plant size, plant growth, fecundity, seed ratio, seed mass and mucilage ratio. For traits for which we had data from several years (plant size, growth and fecundity) we averaged the CV across years.

Environmental variability of populations

In the 11 populations sampled for phenotypic variation, we also estimated annually the density of *P. coronopus* (D) from linear transects (Strong 1966), with the equation $D = \Sigma(1/d) \times (1/T)$, where T is total transect length, and d is the diameter perpendicular to the transect of non-seedling individuals intercepting

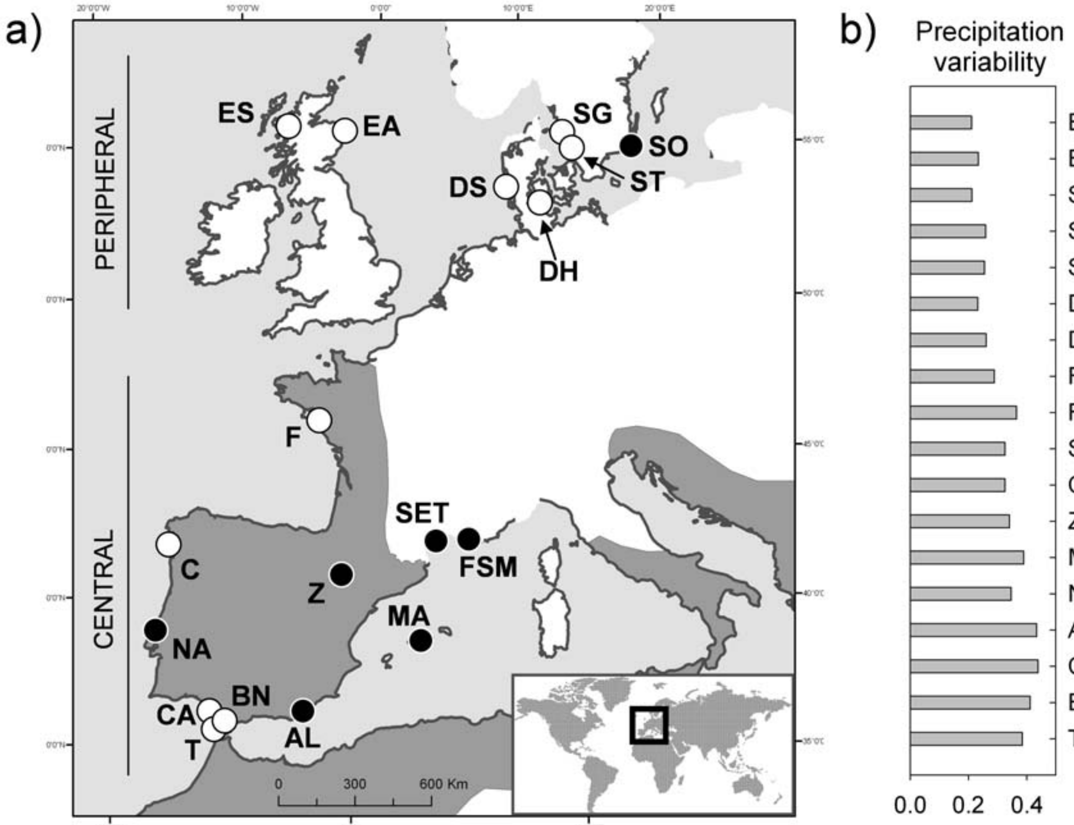

Fig. 1 a) Location of central and northern peripheral populations of *Plantago coronopus* sampled in this study. Black circles correspond to populations sampled for genetic analyses, and white circles to populations subject both to genetic and phenotypic analyses. In grey, geographic distribution of the species, including some coastal outlines and omitting the southernmost area (simplified from Hultén and Fries 1986). b) Precipitation variability in populations (see Material and Methods for details on estimation), ranked by latitude. See Table 1 for acronyms and other information of populations.

the transect. We collected data from 3 yr for peripheral populations and from 4 yr for central populations, and we calculated the CV in annual density as a proxy for variation in intraspecific competition.

Meteorological data were obtained for all 18 populations from several databases: Spanish National Meteorological Agency (populations T, BN, CA, AL, MA and Z), MeteoGalicia (C), MeteoFrance (F), Danish Meteorological Institute (DH and DS), Swedish Meteorological and Hydrological Institute (ST and SG), Met Office (EA and ES) and the website http://www.tutiempo.net (NA, SET, FSM and SO). We obtained annual temperature and annual and monthly precipitation from 10-20 yr within the last four decades (depending on availability) from the nearest meteorological station to each population. Finally, we calculated for each population the CV in annual temperature and three different estimates of precipitation variability: 1) the CV in annual precipitation, used here as a measure of inter-annual variability; 2) the average of the annual Precipitation Concentration Index (PCI; Oliver 1980), which is the ratio between the summatory of the squared monthly precipitation within a year and the squared summatory of monthly precipitation, and reflects intra-annual variability; and 3) the CV of the annual PCI.

Genetic analyses

For all 18 populations, we collected leaf samples of 6-12 individuals per population (Table 1), for a total of 179 individuals. Leaves were collected *in situ* or from individuals grown

Table 1. Populations of *Plantago coronopus* sampled in this study. N corresponds to the number of individuals used for genetic analyses, Fr_t is the total number of AFLP fragments, Fr_p is the percentage of polymorphic fragments and H_D is average gene diversity (± SD). For populations subject to phenotypic analyses (PA), the number of years of data collection is shown.

Population	Coordinates	Habitat	Genetic analyses				PA (yr)
			N	Fr_t	Fr_p	H_D	
Central							
T - Spain	36’02N 05’38W	Sand dune	12	315	62.25	0.224 ±0.11	8
BN - Spain	36’06N 05’32W	Forest gaps	12	335	70.71	0.248 ±0.13	4
CA - Spain	36’25N 06’13W	Sand dune	10	285	59.22	0.211 ±0.11	4
AL - Spain	36’43N 02’11W	Sandy cliff	6	239	45.77	0.200 ±0.11	-
NA - Portugal	39’35N 09’04W	Sand dune	12	286	56.83	0.203 ±0.10	-
MA - Spain	39’46N 03’45E	Sand dune	11	261	52.27	0.194 ±0.10	-
Z - Spain	41’39N 0’50W	Riverside	10	276	57.05	0.215 ±0.11	-
C - Spain	42’33N 09’01W	Sand dune	11	266	53.14	0.196 ±0.10	7
SET - France	43’24N 03’39E	Lagoon rocks	12	285	59.21	0.212 ±0.11	-
FSM - France	43’27N 04’52E	Lagoon rocks	6	214	39.91	0.180 ±0.10	-
F - France	47’18N 02’30W	Sand dune	8	221	41.64	0.167 ±0.09	5
Peripheral							
DH - Denmark	55’08N 09’59E	Coastal prairie	11	215	39.91	0.148 ±0.07	4
DS - Denmark	55’29N 08’15E	Coastal prairie	11	268	48.80	0.179 ±0.09	5
SO - Sweden	56’13N 16’24E	Coastal prairie	10	183	34.92	0.136 ±0.07	-
ST - Sweden	56’23N 12’38E	Coastal prairie	11	205	33.40	0.124 ±0.06	5
SG - Sweden	56’55N 12’21E	Coastal prairie	9	205	31.88	0.120 ±0.06	7
EA - Scotland	57’20N 01’55W	Coastal prairie	11	208	36.22	0.137 ±0.07	4
ES - Scotland	57’30N 06’26W	Coastal prairie	6	151	27.33	0.125 ±0.07	4

in the greenhouse from seeds collected in populations (from different individuals separated by at least 1 m). Plant material was stored in silica gel immediately after collection.

Total genomic DNA was extracted from dry leaves using the unmodified QIAGEN® DNeasy Plant Mini Kit protocol. Quality and quantity of extracted DNA were determined electrophoretically after SYBR green staining using a ladder with known amounts of DNA as standards (HyperLadder™, Bioline). We performed an amplified fragment length polymorphism (AFLP) analysis following established protocols (Vos et al. 1995). An initial screening of selective primers, using 72 primer combinations with three and four selective nucleotides, was performed on a total of eight individuals belonging to eight different populations. The final six primer combinations for the selective PCR were (fluorescent dye in brackets): EcoRI (FAM)-ACT/MseI-CAA, EcoRI (VIC)-AGG/MseI-CTA, EcoRI (NED)-ACC/MseI-CTG, EcoRI (FAM)-ACT/MseI-CTA, EcoRI (VIC)-AAG/MseI-CAT and EcoRI (NED)-AGC/MseI-CAG. MseI primers with four selective nucleotides were chosen for the selective amplification. We replicated 35 individuals (16.6%) to exclude non-reproducible bands and to calculate the error rate according to Bonin et al. (2004). The fluorescence-labelled selective amplification products were separated by capillary gel electrophoresis at the "Genomic Unit" (Universidad Complutense, Madrid, Spain), on an automated sequencer (3730 DNA Analyzer, PE Applied Biosystems, Foster City, CA, USA) with an internal size standard (GeneScan® ¯500 LIZ, Applied Biosystems). Raw data were exported to GeneMarker 1.8 (SoftGenetics LLC, PA USA) for scoring of fragments. The scoring was normalized after different automatic runs with different parameters. The peaks were considered to be present when they were over a scoring fluorescence intensity threshold determined by visual inspection of the electropherograms, and they were reproducible between independent replicates. Amplified fragments from 75 to 500 base pairs were scored. The results of the scoring were exported as a presence/absence matrix.

Genetic diversity was estimated for each locus and population using the formula $H_D = 1 - \Sigma(x_i^{\ 2})$, where x_i is the population frequency of each phenotype "allele" (1 or 0) at locus *i* (software Arlequin 3.01; Excoffier et al. 2005). Then, H_D was averaged across all loci for subsequent analyses (Lowe et al. 2004). We also estimated genetic diversity with two additional metrics calculated with FAMD software: the total number of AFLP fragments presents (Fr_t) and the percentage of polymorphic fragments (Fr_p).

Analysis of phenotypic variation, genetic diversity and correlates

Previous to the analyses of the potential drivers of phenotypic and genetic variation, we performed some preliminary analyses. To test the relationship between the various measures of genetic diversity, we performed a Pearson's correlation test (*cor* procedure, package *stats* in R) between H_D and Fr_t, and between H_D and Fr_p. We also checked for collinearity among the genetic and environmental explanatory variables (H_D, CV in annual density, CV in annual temperature, CV in annual precipitation, PCI and CV in PCI) with an analysis of variance inflation factor (VIF; *vif* procedure, package *car* in R). The three precipitation variables were similar and showed relatively high VIF values (10, 4.9 and 3.1), which can be problematic (Kleinbaum et al. 1988). Thus, we performed a Principal Component Analysis with the three precipitation variables (*prcomp* procedure, package *stats* in R), and the first component explained 80.5 % of the total variance. Hence we calculated from the coefficients of this first component a new variable, hereafter referred as "precipitation variability".

We then analyzed the effect of environmental variability and genetic diversity on phenotypic variation with a Linear Mixed Model (n = 11 populations; *lme* procedure, package *nlme* in R), including H_D, CV in annual density, CV in annual temperature and precipitation variability as covariates, position (central vs. peripheral) as a fixed factor and the type of phenotypic trait as a random factor. To analyze the effect of precipitation variability alone on phenotypic traits, we also performed a Linear Model for each trait (n = 11 populations; *lm* procedure, package *stats* in R). In these analyses, we corrected *p*-values for multiple testing with the false discovery rate method (Benjamini and Hochberg 1995; *p.adjust* procedure, package *stats* in R), which is appropriate for low sample sizes. Finally, we analyzed the factors that might affect H_D with another Linear Model (n = 18 populations), where CV in annual temperature and precipitation variability were the covariates and position was a fixed factor (we did not include density because we only had data for 11 populations and its effect was non-significant).

Results

General patterns of phenotypic variation and genetic diversity

There were differences among phenotypic traits in the magnitude of within-population variation (Fig. 2a), traits measured at the individual level (plant size, growth and fecundity) showing higher variation than those at the seed level (seed mass, mucilage ratio and seed ratio). The three southernmost populations (T, BN and CA) showed in general higher phenotypic variation, but there were no clear differences between central and peripheral populations.

In genetic analyses, the three AFLP primer combinations generated 796 unambiguously scorable fragments, FAM-ACT/CAA: 164, VIC-AGG/CTA: 135, NED-ACC/CTG: 78, FAM-ACT/CTA: 184, VIC-AAG/CAT: 134, NED-AGC/CAG: 101, of which all but one

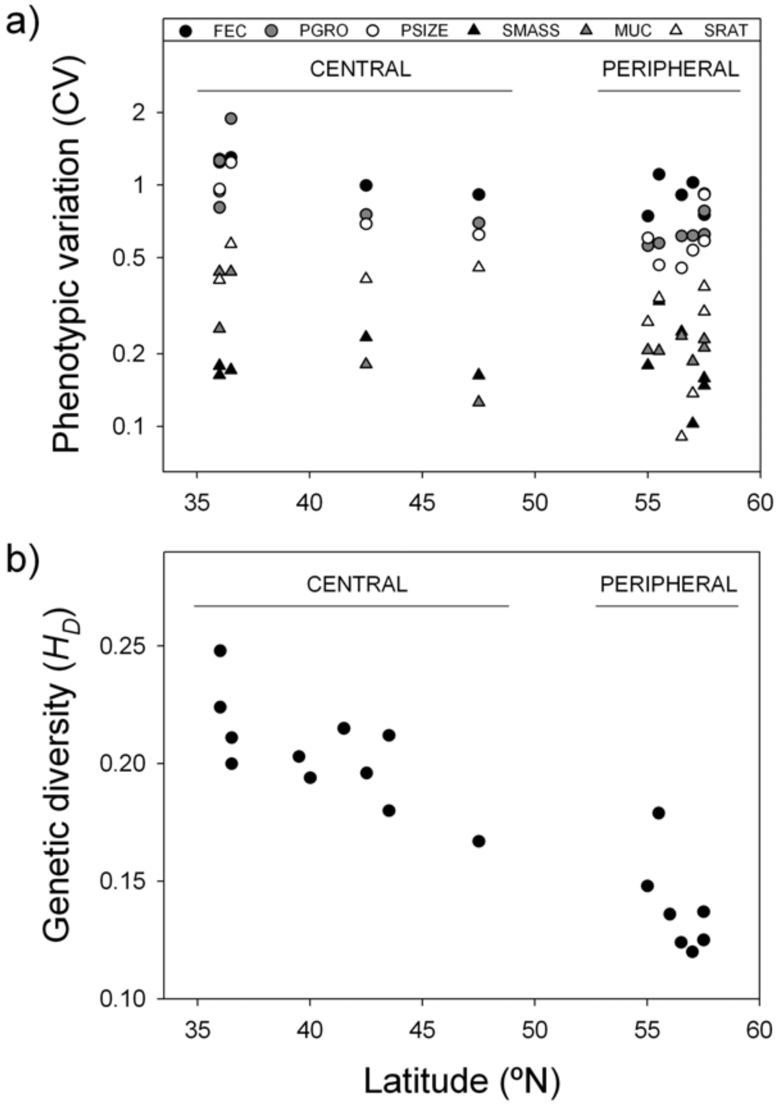

Fig. 2 Phenotypic variation (a), measured with coefficient of variation (CV) in six life-history traits, and genetic diversity (b), estimated with H_D, in central and peripheral populations of *Plantago coronopus* along the latitudinal gradient. In a), abbreviations correspond to traits: fecundity (FEC), plant growth (PGRO), plant size (PSIZE), seed mass (SMASS), mucilage ratio (MUC) and seed ratio (SRAT).

were polymorphic. All 273 investigated individuals had unique AFLP profiles. The error rate, based on phenotypic comparisons among the 35 replicated individuals, amounted to 2.8 %. For subsequent genetic analyses, we selected the polymorphic bands with a percentage variation lower than genotyping error, obtaining 461 polymorphic bands.

H_D was highly and positively correlated to the other measures of genetic diversity, *i.e.*, Fr_t ($t_{16} = 9.52$, $p < 0.001$, $r = 0.92$) and Fr_p ($t_{16} = 14.29$, $p < 0.001$, $r = 0.96$), which indicates that H_D can be used as a reliable estimator of genetic diversity. Northern peripheral populations, located in Denmark, Sweden and Scotland, showed the lowest genetic diversity values, whereas central populations had higher values, especially in South Spain (Table 1, Fig. 2b).

Correlates of phenotypic variation and genetic diversity

Phenotypic variation was significantly correlated to precipitation variability, but density variation, temperature variability, H_D and position showed no significant effects (Table 2). The effect of precipitation variability on phenotypic variation differed depending on the phenotypic variable (Fig. 3). Precipitation variability was significantly and positively correlated with variation in plant size, fecundity, growth, mucilage ratio and seed ratio, the latter showing the lowest R^2 value. Variation in seed mass was not significantly affected by precipitation variability. Precipitation variability showed a gradual decline in the latitudinal gradient, from the central to the northern peripheral populations (Fig. 1b).

The analysis of genetic diversity showed that position exerted a marginally significant effect on H_D, whereas neither precipitation variability nor temperature variability had a significant effect (Table 2). When non-significant covariates were removed from the analysis, the effect of position on H_D became significant ($t_{16} = -6.41$, $p < 0.001$).

Discussion

Understanding life-history variability in species requires the identification of the evolutionary and demographic processes operating on populations (Lynch et al. 1999, Reed and Frankham 2001, Mitchell-Olds and Schmitt 2006). In this study, we analyzed genetic and phenotypic variation within populations across the latitudinal gradient of *P. coronopus* in Europe, in relation with environmental and geographical factors. Our analyses showed that the simple and intuitive relationship between phenotypic variation measured on fitness-related traits, and genetic diversity inferred from neutral molecular markers, does not hold in this species. Phenotypic variation within populations was mainly shaped by precipitation variability, suggesting adaptive variation, whereas genetic diversity was correlated with the central *vs*. peripheral position of populations, probably in close relation with the demographic history of the species.

Table 2. Analyses of correlates of phenotypic variation and genetic diversity in *Plantago coronopus*. Fixed effects correspond to precipitation variability (PrVar), CV in annual density (CV_{dens}), CV in annual temperature (CV_{temp}), genetic diversity (H_D) and position (central *vs*. peripheral). The analysis of phenotypic variation includes a random effect of type of phenotypic trait. In bold, *p*-values that are significant (< 0.05) or marginally significant (< 0.1).

Analysis	Fixed effects	Coefficient	*t*	*p*
Phenotypic variation	PrVar	2.22 ± 0.72	3.10_{54}	**0.003**
	CV_{dens}	0.05 ± 0.09	0.54_{54}	0.592
	CV_{temp}	-1.46 ± 1.07	-1.36_{54}	0.179
	H_D	-0.21 ± 1.23	-0.17_{54}	0.867
	Position	0.20 ± 0.13	1.49_{54}	0.142
Genetic diversity	PrVar	0.21 ± 0.13	1.63_{14}	0.126
	CV_{temp}	0.11 ± 0.21	0.53_{14}	0.604
	Position	-0.05 ± 0.02	-1.91_{14}	**0.076**

Plantago coronopus showed values of genetic diversity similar to other widespread short-lived perennials, and higher than plants with the same life form but narrower ranges (Hamrick and Godt 1996). Genetic diversity within populations was negatively correlated with peripherality, populations showing a decline in H_D from the range centre in the Mediterranean region to the range edge in countries of N Europe. Changes in genetic diversity along geographical gradients are commonly associated with processes such as genetic drift, reduced gene flow and founder effects (Lesica and Allendorf 1995, Vucetich and Waite 2003), which could have eroded the genetic pool in the northern range margin of *P. coronopus*. Such decline in genetic diversity in peripheral populations is indeed a frequent pattern in comparative analyses across species' ranges (see Eckert et al. 2008 for review). It is interesting to note that current northern populations of *P. coronopus* show higher densities than central ones (Villellas et al. 2012). Thus, the lower genetic diversity found in these populations might respond to smaller population densities in the past, and/or to isolation. Divergences between present demographic and genetic patterns have also been reported for the perennial herbs *Lychnis viscaria* (Lammi et al. 1999) and *Cirsium heterophyllum* (Jump et al. 2003), and call for caution when using information from one component of species' biology to infer patterns in other components.

Phenotypic variation within populations was not related in *P. coronopus* with neutral genetic diversity. Several studies have shown a similar lack of correspondence between genetic diversity and variation in life-history traits in plants (*e.g.* Waldmann and Andersson 1998, McKay et al. 2001), and Reed and Frankham (2001) concluded that molecular measures of genetic diversity constituted poor predictors of adaptive genetic variability. In our study, phenotypic variation was instead highly correlated to temporal fluctuations in local

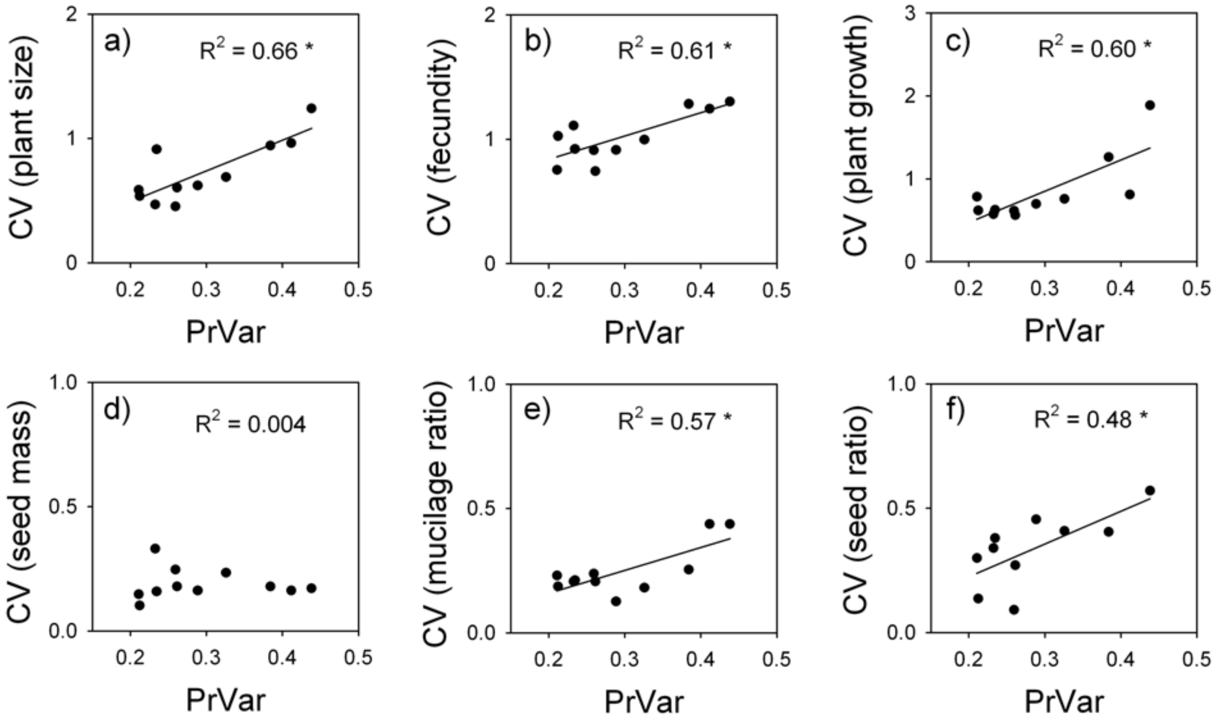

Fig. 3 Relationship between phenotypic variation in life-history traits within populations of *Plantago coronopus*, measured as coefficient of variation (CV) among individuals, and precipitation variability (PrVar; see Material and Methods for details on the estimation). Traits are a) plant size, b) fecundity, c) plant growth, d), seed mass e) mucilage ratio and f) seed ratio. R^2 values are given for each regression analysis, and the statistical significance is represented by asterisks: * $p < 0.05$ (corrected by the false discovery rate method).

precipitation, suggesting that selective forces have promoted life-history variability within populations. This result indicates that variability in environmental parameters, such as precipitation, may be used to infer evolutionary potential within populations. Variation in environmental conditions has been similarly proposed as a useful surrogate for trait divergence among populations (Knapp and Rice 1998, Bekessy et al. 2003, Bottin et al. 2007) and also to detect areas of high species diversity (Faith 2003, Sarkar et al. 2005).

Phenotypic variation was estimated in this study in natural populations, and thus it may include both the effects of adaptive genetic variation and phenotypic plasticity. Indeed, both sources of variation seem to be present in *P. coronopus*: Wolff (1991a, 1991b) reported significant levels of genetic variation within populations, but also found evidences of plasticity (see also Waite and Hutchings 1982, Smekens and van Tienderen 2001). However, phenotypic plasticity itself can also be considered a trait where selection acts (Schlichting 1986, Thompson 1991, Pigliucci 2005), so we expect both genetic variation and plasticity to increase under selective forces such as environmental variability (Rice and Emery 2003, Lande 2009, Dawson et al. 2011). Doubtless, analyses of heritability with *P. coronopus* at the same continental scale as this study would help to quantify both phenomena separately.

Our analyses highlight the importance of precipitation in shaping life-history and demographic variability within populations of *P. coronopus*. This climatic variable has indeed a similarly important role in the differentiation among populations (Villellas et al. 2012, Villellas and García 2012, Villellas et al. *in press*). Seed-related traits in particular, whose variation across populations is mediated by a trade-off between fecundity and the resources allocated to seed tolerance to stress (Villellas and García 2012), seem to be highly sensitive to precipitation regime in this species. Seed mass was the only trait in our study that remained virtually unaffected by environmental variability. However, considering the seed dimorphism of *P. coronopus*, variation in average seed mass may also be regulated in practice through the ratio between big basal and small apical seeds. The correlation between precipitation and variation in plant size and growth, in turn, may take place through different demands on resource acquisition, or indirectly through the close association between plant size and seed production (Villellas and García 2012). Overall, the differences among traits in their response to environmental variability highlight the importance of using several components of phenotypic variation, fitness-related traits usually being of more interest than purely morphological characters (Reed and Frankham 2001).

The combination of ecological, phenotypic and genetic information is crucial for analyzing the patterns and causes of trait variation within taxa, and for evaluating their future adaptive potential (Crandall et al. 2000, Bekessy et al. 2003, Narbona et al. 2010). Our study of a widespread plant at a continental scale showed that phenotypic variation within populations was neither correlated with genetic diversity inferred from molecular markers, nor with the position of populations within the species' range. Instead, phenotypic variation was moulded by precipitation variability, suggesting that populations may have a higher adaptive potential in variable rather than stable environments. The use of environmental variability as a proxy for evolutionary potential could be considered in some conservation tools, such as niche-models predicting the future distribution of plants under environmental changes (Botkin et al. 2007), to improve the management of biodiversity.

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General discussion

General discussion

In this study we have analyzed demographic, life-history and genetic variation in the widespread herb *P. coronopus* through most of its latitudinal range, from data gathered over several years of field and laboratory work. Our results agreed with classical central-marginal hypotheses in some aspects, such as the genetic pattern, but not in others, such as density, demographic variability, and overall population performance. In fact, environmental conditions seemed to have a higher influence on plant performance than the position of populations within the species' range. Variation in demographic patterns and reproductive traits at continental and regional scales, and both among and within populations, were indeed closely linked to some biotic and abiotic factors, particularly precipitation regime. Overall, our study highlights the versatility of *P. coronopus* in response to variation in environmental conditions, and complements similar findings of previous research on the same taxon at smaller spatial scales (Waite and Hutchings 1982, Waite 1984, Braza et al. 2010, Braza and García 2011). Such life-history variability seems to be a key factor for widespread plants to extend over large and heterogeneous ranges.

1. Factors influencing population performance across species' ranges

Peripheral populations are traditionally predicted to show, with respect to central ones, a worse and more variable demographic performance (Hengeveld and Haeck 1982, Brown 1984, Lawton 1993, Lesica and Allendorf 1995, Vucetich and Waite 2003), lower genetic diversity and higher genetic differentiation from other populations (see references in Brussard 1984, Wilson et al. 1991). However, our study has provided some diverging results regarding the central-marginal pattern. On the one hand, northern peripheral populations of *P. coronopus* showed as expected lower genetic diversity with respect to central ones (see Chapter 4), and higher genetic differentiation in the periphery (mean values of genetic differentiation of each population with respect to the others, F_{ST}, ranged from 0.31 to 0.38 in peripheral populations, and from 0.23 to 0.30 in central ones; *unpublished results*). On the other hand, northern peripheral populations showed higher densities, and there was no consistent geographic pattern in vital rates' means and variabilities (see Chapter 1). Furthermore, the differences found in vital rates led to no significant differences among regions in the stochastic growth rate (see Chapter 2), a metric that represents general population performance much better than individual fitness components (Caswell 2001).

Thus, our study confirmed central-marginal hypotheses from a genetic perspective, but not regarding demography. The first general conclusion is that theoretical predictions should not be assumed without testing, and that models that fit under a certain scientific discipline should not be indiscriminately applied to others.

The failure of widely accepted ideas in predicting the demographic performance of *P. coronopus* suggests that plant populations may follow species-specific rather than generalizable patterns throughout ranges. This view is indeed becoming increasingly patent in the literature, as recent reviews have failed to find consistent differences between central and peripheral populations regarding density, vital rates or demographic fluctuations (Sagarin and Gaines 2002, Gaston 2003, 2009, Sexton et al. 2009). The idiosyncrasy in population performance shown by *P. coronopus* and other plants seems to respond to particular environmental patterns across ranges, which do not necessarily imply worse conditions towards the periphery. Much of the theory underlying central-marginal models is based indeed on the assumption of lower habitat suitability in range edges (Lawton 1993, Lesica and Allendorf 1995). However, peripheral populations may occur in locally favourable patches within a generally unsuitable matrix (Holt and Keitt 2000, Lennon et al. 2002). It is important thus to consider not only the geographical location of populations, but also their position within the species' ecological niche, which includes the main environmental factors affecting plants. In this way, we will be able to discern whether geographically marginal populations are also ecologically marginal and vice versa (Soulé 1973, Grant and Antonovics 1978).

In relation with ecological marginality, one should also bear in mind that species' life cycles combine vital rates that individually may be affected by different environmental factors, so that environmental conditions that are favourable for a certain set of vital rates may be negative for another (Mandujano et al. 2001). This is likely the case for *P. coronopus*, since the low intraspecific competition in sand dunes compared with that of coastal meadows seems to favour growth and fecundity in central populations, whereas the higher water availability in northern locations appears to enhance seedling recruitment (see Chapter 1). Hence, the ecological centrality *vs*. marginality of populations should be evaluated by carefully considering the consequences of environmental factors on each particular vital rate. In the case of *P. coronopus*, for example, northern peripheral populations were not ecologically marginal, at least as concerns conditions for seedling recruitment.

The effects of environmental conditions on the intraspecific variability of *P. coronopus* became apparent in our study both in population and individual performance. One of the most illustrative results at the population level was the finding of the same pattern of demographic differentiation within central and northern peripheral areas of the species' range, in response to environmental factors. Mean annual values and variability in precipitation seemed indeed to determine, in the same way within both regions, how differences among populations in vital rates contribute to differences in stochastic growth rates (see Chapter 2). This suggests that certain demographic strategies may be inherent or characteristic of each set of environmental conditions, independent of the geographical location of populations. This seems indeed a common phenomenon in widespread plants, since population structure and density of *Viola elatior* and *V. stagnina* also varied in same way as a result of management within peripheral and core regions (Eckstein et al. 2004), and density patterns in the invasive *Centaurea melitensis* showed similar responses to disturbance and precipitation in its native and novel ranges (Moroney and Rundel 2012). In some cases, however, different factors across the range may be responsible for within-region variation in plant performance (Wagner et al. 2011).

Besides population-level parameters, individual life-history traits showed also a high variation in relation with varying environmental conditions. For example, seed size, a key trait for plant dispersal, germination and seedling survival (Westoby et al. 1992, Chapin III et al. 1993, Coomes and Grubb 2003), showed in *P. coronopus* considerable variation along the environmental gradient (see Chapter 3). In fact, although seed size has been traditionally regarded as a relatively fixed trait within species (Harper et al. 1970), there is growing evidence for the opposite pattern (McWilliams et al. 1968, Baker 1972, Susko and Lovett-Doust 2000, Moles and Westoby 2003), and especially in widespread short-lived taxa (Völler et al. 2012). Regarding the partition of trait variance in *P. coronopus*, reproductive traits varied more within than among populations, according to a complementary analysis of variance (percentages of variance within and among populations were, respectively, 80% and 20% in seed production per plant, 59% and 41% in seed production per fruit, 51% and 49% in basal seed mass, and 74% and 26% in mucilage production; *unpublished results*). This result seems to be common in plant taxa (Venable and Burquez 1989, Méndez 1997, Pluess et al. 2005, Völler et al. 2012), and suggests that gene flow among populations may have homogenized to some extent the genetic pool for those traits. In any case, as commented above, this would have not impeded *P. coronopus* to adjust its phenotype to the local conditions throughout its range.

Several environmental factors have been analyzed in our study, such as temperature, precipitation, soil richness and intraspecific competition, and all of them showed some effects on the biology of *P. coronopus*. However, precipitation (as a proxy for water availability) seemed to exert the largest influence on its intraspecific variability, both among and within populations. This is not surprising since many studies have shown the relevance of precipitation and water availability for plant biology (Baker 1972, O'Connor 1994, Smith et al. 2005, Franks and Weis 2008). Following our results, we hypothesize that the main effect of precipitation takes place through its influence on recruitment, a key process in short-lived plants (Verkaar and Schenkeveld 1984, Picó et al. 2003, García et al. 2008). In central populations, where water availability is scarcer or more unpredictable, the species seems to have developed two different strategies (see Chapter 3) to increase the otherwise failing recruitment: 1) improving the tolerance of seeds to water stress through a larger size, a thicker mucilage coat, and a higher abundance of basal seeds, and 2) increasing the total number of seeds per plant, through larger plant sizes that allow an increase in the number of fruits (although the number of seeds per fruit decreases due to a trade-off with seed size). In addition, from a demographic perspective, recruitment was highly correlated with density of adult individuals (see Chapter 1), and constituted the most relevant vital rate for stochastic population growth rates (see Chapter 2). Thus, precipitation regime (through its influence on recruitment) seems to promote changes not only in individual life-history traits such as plant size, seed size and seed production, but also in several population parameters, becoming a major driver of variation across the range of *P. coronopus*.

2. Life-history variability: the key to success in widespread plants

Plantago coronopus has proved to be a highly versatile plant in various ways along the steep environmental gradient present from North Africa and South Europe to North Europe. In the first place, the species showed a correlation between inter-individual variation in life-history traits and the level of environmental variability experienced by populations (see Chapter 4). Sites with the highest precipitation variability in our study, mainly in southern Europe, contained indeed the highest within-population variability in reproductive and vegetative traits (fecundity, seed traits and plant growth), whereas the most stable conditions in northern locations seemed to favour a higher uniformity in such traits among individuals.

Another mechanism of the species to cope with the environmental gradient is to reduce the risk of failure in places with variable and unpredictable conditions, through the so-called bet-hedging strategies (Cohen 1966, Philippi and Seger 1989). Such strategies may be indeed especially characteristic of short-lived plants (Seger and Brockman 1987, Mandák 1997). For example, seed dimorphism, which allows plants to diversify the chances of offspring success (Imbert 2002), is further accentuated in *P. coronopus* in the more unpredictable central locations (see Chapter 3): the characteristics of apical seeds (mostly “losers” that play an important role only under certain conditions; Braza and García 2011) remained unchanged with respect to peripheral populations, whereas an increase in size and mucilage production was observed in basal seeds (mostly “winners”, since population growth basically relies on them). In addition, plants from central populations produce a larger number of fruits and fewer seeds per fruit. Considering that fruits themselves may constitute diaspores (*personal observation*), this would also help to spread seed germination in space and time, and reduce the risk of offspring failure.

Finally, *P. coronopus* presented also a high versatility in the arrangement of the life cycle. First, we found compensatory changes among vital rates, both between and within central and peripheral areas, without implying clear increases or decreases in stochastic population growth rates (see Chapter 2). In addition, the species varied in the timing of the first reproductive event: plants in central populations became reproductive in their first year relatively frequently (mean annual percentages range from 6% to 45%), whereas such yearling reproduction was virtually absent in most peripheral populations (see Chapter 2). These differences in age at first reproduction, a key parameter in plant life-history (Cole 1954), may be explained by the tendency for higher individual growth in central locations (see Chapters 1, II), which would allow plants to reach earlier the threshold size for producing seeds. Similar changes in age-specific demography have been also reported for other widespread plants, both among (Reinartz 1984) and within populations (Roach 2003).

These findings add to previous knowledge of the variability of *P. coronopus* in different biological aspects, such as the existence of annual and perennial populations (Chater and Cartier 1976), or high variation in outcrossing rates (Wolff et al. 1988), resource allocation (Waite and Hutchings 1982), and morphological traits (Dodds 1953). Overall, our study suggests that *P. coronopus*, and perhaps other widespread plants, may achieve their large distribution ranges through variation in several ecologically relevant traits, both among and within populations, and through changes in demographic and life-history strategies at different spatial scales.

3. The importance of large-scale integrative analyses

Few detailed ecological studies focused on particular organisms have been carried out at large temporal and/or spatial scales (but see Reinartz 1984, Horvitz and Schemske 1995, Menges and Dolan 1998, Angert 2009, Doak and Morris 2010, Wagner et al. 2011). However, large-scale approaches are very necessary to fully understand the ecology and demography of species, and their intraspecific variability. For example, determining the intensity of temporal fluctuations and their long-term effects on population performance is very important in places with high environmental stochasticity, especially in a context of expected increases in climatic variability due to global warming (Karl and Trenberth 2003, Salinger 2005). In *P. coronopus*, we found indeed that the effect of variability in some vital rates had important consequences in the stochastic growth rates of several populations (see Chapter 2), and Braza and García (2011) highlighted the importance of measuring recruitment over several years in this species to properly understand the role of dimorphic seeds.

Regarding spatial scales, the among-population variability can only be captured by prospecting a large area of species' distribution ranges. Inferring the demographic behaviour from one or a few populations has proved indeed misleading (Frederiksen et al. 2005), and the high variability found in *P. coronopus* at both continental and regional scales undoubtedly confirms this point of view. Ideally, multiple spatial scales should be considered, as there is evidence of intraspecific variation in plant performance at a huge range of levels, from the global (Williams 2009) to the very local scale (Miller and Fowler 1994). The present study, carried out at both continental and regional scales, complements previous research with *P. coronopus*, which also showed life-history variability at more local scales (Waite and Hutchings 1982, Waite 1984, Braza et al. 2010, Braza and García 2011).

Besides large spatio-temporal approaches, the results found in this study showed the importance of analyzing different sources of information. We have already discussed the discrepancies between demographic and genetic patterns across the distribution of *P. coronopus*. In addition, environmental factors seemed to exert many times a higher influence on plant performance than the position of populations within the range, as seen above. Finally, several components of the life cycle responded in different ways to local environmental conditions. Thus, in agreement with previous studies (Oostermeijer et al. 2003, Leimu et al. 2006, Montesinos et al. 2009, Noël et al. 2010), we highlight the necessity of integrating environmental, geographical, demographic and genetic data, and the widest possible range of traits, to fully understand intraspecific variation in plant performance. This might be particularly useful when managing peripheral populations and analyzing their demographic status and evolutionary potential (Bunnell et al 2004, Gapare et al. 2005).

4. What is next? Considerations for future work

The present study has focused on the northern periphery due to logistic and temporal limitations, although other margins of the distribution range could show different patterns. Divergences in demographic performance have been indeed found between northern and southern boundaries in several US tree species (Purves 2009) and in the short-lived weed *Verbascum thapsus* (Reinartz 1984). From a phylogeographic perspective, northern populations may constitute since last glaciations the leading edge of many species in the northern hemisphere (Hewitt 1999, Travis and Dytham 2004), whereas southern parts may remain as the rear edge. Thus, an open question of our study system is whether demographic and genetic patterns in the southern range margin of *P. coronopus* are similar to those in the north. Indeed, the rear edge may also have a relevant role in the ecology and evolution of species (Hampe and Petit 2005). On the other hand, populations at the eastern margin might not be expected to behave so differently from central ones, since longitudinal gradients usually imply smaller environmental changes. However, testing predictions from central-marginal theories across the longitudinal gradient would provide a more reliable picture of range-wide species performance.

We have not analyzed genetic differentiation among populations in depth yet, which could help us to understand processes such as gene flow and isolation among populations (Slatkin 1987). Such information would also allow us to test whether differences in life-history traits among populations are more correlated to the degree of neutral genetic differentiation or to environmental selective factors, as analyzed at the within-population level. In addition, another interesting issue for future work would be to determine the relative role of phenotypic plasticity and local adaptation in the observed intraspecific variation in *P. coronopus*. Ecotypic differentiation has been reported indeed for some demographic and life-history traits in the congener *P. lanceolata* (Van Tienderen and Van der Toorn 1991, Shefferson and Roach 2012) and in other widespread plants (Bennington and McGraw 1995, Joshi et al. 2001, Santamaría et al. 2003), and we have carried out some transplant experiments that will help us to analyze this process in *P. coronopus*.

Despite limitations, our study has shown the tremendous variability present across the range of a widespread plant, which contrasts with the frequent view of species as uniform. This consideration calls for including intraspecific variation in comparative analyses of ecological and demographic traits across taxa (Frederiksen et al. 2005). In addition, it may also improve niche-model predictions of future distribution and abundance of taxa (Pearman et al. 2010), since unique species-specific responses to the upcoming global changes cannot be assumed any longer.

Conclusions

Conclusions

1. In this thesis, we analyzed variation in demographic and life-history traits of the widespread short-lived herb *Plantago coronopus* over several years and across most of its latitudinal range, considering the effects of the central *vs*. peripheral position of populations, the main environmental factors, and genetic diversity. This large-scale spatio-temporal approach provided a representative picture of the natural variability present in the species. In addition, the combination of different sources of information, and the analysis of a wide range of life cycle components, allowed us to understand the patterns and causes of such intraspecific variation, and to test the validity of some ecogeographical and genetic models.

2. Northern peripheral populations of *P. coronopus* showed lower fecundity and lower genetic diversity with respect to central ones. However, northern populations had higher densities, higher recruitment rates, and no differences in either stochastic population growth rates or temporal variability of vital rates compared with central populations. Thus, our study confirmed classical predictions of a lower population performance in range edges as concerns genetic patterns, but not regarding demography. These discrepancies call for caution when using information from one component of a species' biology to infer patterns in other components.

3. A similar trend of demographic differentiation among populations was found within central and peripheral areas, in close relationship with variation in precipitation regime. These results suggest that demographic strategies may be characteristic of certain environmental settings, with independence of the geographical location of populations.

4. A steep environmental gradient along the latitudinal range of *P. coronopus* seemed also to underlie among-population variation in reproductive traits at two different levels. At the fruit level, we found a trade-off between the number of seeds and the allocation of resources to increase their stress tolerance. At the individual level, variation in plant fecundity would allow a further adjustment of the life cycle to the local environmental conditions.

5. Phenotypic variation within populations in several vegetative and reproductive traits showed no correlation with genetic diversity, and was instead correlated with precipitation

variability, suggesting adaptive selection. Genetic diversity was related to the location of populations within the species' range, probably as a result of past demographic processes that would have eroded the genetic pool in the northern periphery.

6. Precipitation emerges as the most relevant environmental factor for life-history and demographic variation across the range of *P. coronopus*, mainly through its observed effect on recruitment. Firstly, differences in recruitment success among populations appear to trigger variation in several life-history traits, such as seed production, seed traits and plant size. In addition, recruitment seems to have a key role in the differences in densities and stochastic growth rates among populations.

7. Overall, environmental conditions seemed to have a higher influence in life-history and demographic variation of *P. coronopus* than the central *vs*. peripheral position of populations. Thus, we advocate for a clear distinction between geographical periphery and ecological marginality in studies across species' ranges. In addition, the marginality of populations should be evaluated by considering the consequences of environmental factors on each particular vital rate, as conditions in each region may be detrimental for some rates but favorable for others.

8. *Plantago coronopus* is a widespread herb with a remarkable variation in ecologically relevant traits, both among and within populations, and in demographic and life-history patterns at different spatial scales. The species presents different mechanisms to cope with the steep environmental gradient present from North Africa to North Europe, such as bet-hedging strategies associated with seed production, and compensatory changes in vital rates. Such high ecological and demographic versatility seems to be the key to success in widespread plants over their large and heterogeneous ranges, and should be considered in niche-models predicting the future distribution and abundance of species.

Resumen

Resumen

1. Introducción general y objetivos del estudio

Las especies de amplia distribución han recibido tradicionalmente menor atención que las especies raras o endémicas, a pesar de que son también relativamente poco frecuentes, y presentan en algunos casos un claro declive en sus poblaciones. Por otra parte, las especies de amplia distribución tienen una gran importancia ecológica, por ejemplo en la estructura y el funcionamiento de los ecosistemas. Por tanto, el estudio de las características que permitirían a estos organismos expandirse a lo largo de extensos rangos tiene un gran interés desde un punto de vista tanto teórico como aplicado.

Las plantas de amplia distribución parecen tener algunas características reproductivas típicas, como una predominancia de la reproducción sexual y una gran capacidad de dispersión, además de mayores tasas de crecimiento poblacional en comparación con taxones de distribución restringida. Una de las hipótesis más frecuentes para explicar el éxito de las plantas de amplia distribución es la posesión de una gran amplitud de nicho, y por tanto de una gran variabilidad ecológica, demográfica y de historia vital (del inglés, *life history*), y posiblemente una gran variabilidad genética. Sin embargo, la literatura científica muestra evidencias contradictorias respecto a estas generalizaciones.

Los gradientes geográficos y medioambientales son escenarios muy apropiados para entender las características y el funcionamiento de las plantas de amplia distribución. Por una parte, numerosos estudios han demostrado importantes efectos de la variación en el clima, las características del suelo, o el estrés ambiental, a lo largo de gradientes espaciales, sobre diversos atributos de las plantas. Por otra parte, las fluctuaciones temporales en estos factores medioambientales ejercen un papel fundamental en la evolución de las *life history* y en la demografía de las plantas, aunque todavía se necesitan análisis pormenorizados sobre el efecto de la variación de las tasas vitales sobre las tasas de crecimiento poblacional.

La posición de las poblaciones dentro del rango de distribución de las especies y los efectos de esta posición sobre el comportamiento de las mismas constituyen un objeto recurrente de debate. Tradicionalmente se ha predicho un peor funcionamiento de las poblaciones periféricas, ya que se asumen unas condiciones ambientales más desfavorables en la periferia respecto a la parte central. Sin embargo, recientes revisiones han encontrado una ausencia de patrones generalizados en cuanto a comportamiento demográfico, aunque parece haberse confirmado la hipótesis de una menor variación genética en las poblaciones periféricas. En este contexto, la catalogación de las poblaciones como periféricas o marginales en base a factores ecológicos y medioambientales, y no sólo geográficos, podría ser de gran ayuda. Por último, el análisis comparativo de la magnitud y las causas de la variación fenotípica *vs*. genética en las poblaciones centrales y periféricas puede ser de gran utilidad para esclarecer procesos históricos y de adaptación en las especies de amplia distribución.

Para este estudio, hemos elegido una especie de amplio rango geográfico y corta vida: *Plantago coronopus* L ssp. *coronopus*. Se trata de una planta herbácea presente en Europa, el norte de África y el suroeste de Asia, en una gran diversidad de hábitats. La especie presenta poblaciones anuales y perennes, y una gran variabilidad en características como la morfología de las hojas, el sistema reproductivo (ginodioecia), o la tasa de autogamia. Además, *P. coronopus* produce dos tipos de semillas con diferentes características morfológicas y ecológicas. Por último, diversos estudios han encontrado que las tasas vitales de la especie se ven afectadas por factores intrínsecos, como el tamaño de planta o la densidad de individuos, y extrínsecos, como la disponibilidad de agua o nutrientes.

Para entender de manera integral las causas de variabilidad intraespecífica en caracteres fenotípicos o del ciclo vital, se necesitan análisis con escalas espacio-temporales amplias. Por ello, en este estudio examinamos la variación demográfica, genética y de historia vital en 22 poblaciones de *P. coronopus* a lo largo de gran parte de su rango latitudinal. Además, llevamos a cabo una monitorización demográfica intensiva durante cuatro años en cuatro poblaciones del centro del área de distribución de la especie, y seis poblaciones en la periferia norte, donde recogimos datos de campo. En estas poblaciones, y en otras poblaciones adicionales en Europa y el norte de África, también recolectamos material para los análisis genéticos y de producción de semillas. Finalmente, aprovechamos la información de estudios previos con *P. coronopus* para ampliar aún más el rango espacial y temporal del trabajo.

Como objetivos concretos de esta tesis, pretendemos 1) testar las teorías clásicas asociadas al comportamiento de las poblaciones centrales y periféricas en cuanto a densidad, tasas vitales y fluctuaciones temporales en las mismas, y tasas de crecimiento poblacional; 2) analizar el efecto de las condiciones ambientales en el comportamiento general de las poblaciones y en caracteres de relevancia ecológica como el tamaño de planta, la fecundidad y el tamaño de las semillas; y 3) explorar las causas de la variación fenotípica y genética dentro de las poblaciones, considerando como factores las condiciones medioambientales y la posición geográfica de las poblaciones. El objetivo global es analizar la variación demográfica y de historia vital en *P. coronopus*, en relación con factores geográficos, ambientales y genéticos, con el fin de obtener una mejor comprensión de las causas que determinan el éxito de las especies de amplia distribución.

2. Publicaciones

Capítulo 1

Tradicionalmente se ha considerado que las poblaciones periféricas de las especies presentan menores tasas vitales, mayores fluctuaciones demográficas y menores densidades que las poblaciones centrales. Sin embargo, investigaciones recientes han cuestionado la generalidad de tales patrones geográficos. Con el fin de testar estas hipótesis, monitorizamos cinco poblaciones centrales y seis poblaciones de la periferia norte de una planta herbácea de amplia distribución (*Plantago coronopus*) a lo largo de la costa atlántica europea durante 5 años. Estimamos la densidad poblacional y calculamos los valores medios y la variabilidad temporal de cuatro tasas vitales (supervivencia, crecimiento individual, fecundad y reclutamiento) en centenares de plantas en parcelas permanentes dentro de cada población. Las poblaciones centrales mostraron una mayor fecundidad, mientras que el reclutamiento fue mayor en las poblaciones periféricas, indicando un mayor éxito reproductivo final en la periferia. Las poblaciones centrales mostraron mayores tasas de crecimiento individual (marginalmente significativo) que las periféricas, y no hubo diferencias entre ambas posiciones del rango en cuanto a supervivencia. La fecundidad y el crecimiento se vieron afectadas por la competencia intraespecífica, y el reclutamiento por la precipitación, resultados que destacan la importancia de las condiciones ambientales locales para el comportamiento de las poblaciones. Las poblaciones centrales y periféricas no mostraron diferencias significativas en cuanto a la variabilidad temporal en las tasas vitales. Finalmente, la densidad fue significativamente mayor en las localidades periféricas, en discrepancia con el *abundant-centre model* (modelo del “centro abundante”). La densidad mostró una correlación con el reclutamiento, el cual compensaría en las poblaciones periféricas la menor fecundidad y la tendencia hacia un menor crecimiento de las plantas ya establecidas. Tales compensaciones entre tasas vitales podrían ser comunes en taxones de amplia distribución, y desacreditan posibles asunciones simplistas sobre el comportamiento de las poblaciones a lo largo del rango de distribución de las especies. Los análisis demográficos deberían considerar el ciclo vital entero de las plantas, ya que el *fitness* de las poblaciones puede venir determinado por ajustes entre diferentes tasas vitales. Nuestros resultados muestran también la importancia de distinguir entre periferia geográfica y marginalidad ecológica. En un contexto de cambios en la distribución de las especies motivados por el clima, estas consideraciones son cruciales para la fiabilidad de los modelos de nicho y para la gestión de las poblaciones periféricas.

Capítulo 2

Analizar la variación intraespecífica en la dinámica poblacional en relación con los factores medioambientales es crucial para entender la distribución presente y futura de las plantas. Dentro del área de distribución de las especies, con frecuencia se predice que las poblaciones periféricas presentan unas menores y más variables tasas vitales que las poblaciones centrales, aunque se suele desconocer cómo contribuyen estas tasas vitales a las diferencias registradas en las tasas de crecimiento poblacional. Además, se han llevado a cabo pocos estudios a escala tanto continental como regional que consideren la estocasticidad ambiental. En el presente trabajo, calculamos la tasa de crecimiento estocástico en cinco poblaciones centrales y seis poblaciones de la periferia norte de una especie de amplia distribución y corta vida, *Plantago coronopus*, a lo largo de la costa atlántica en Europa. Para evaluar a dos escalas espaciales (continental y regional) cómo los valores medios y la variabilidad de las tasas vitales (fecundidad, reclutamiento, supervivencia, crecimiento y decrecimiento) contribuyeron a las diferencias en la tasa de crecimiento poblacional estocástico, realizamos un análisis SLTRE (del inglés, *Stochastic Life Table Response Experiment*) entre las regiones central y periférica y dentro de cada una de ellas. También analizamos las correlaciones entre las contribuciones de las tasas y las condiciones ambientales locales. Las poblaciones periféricas mostraron unos valores menores y una mayor variabilidad en algunas tasas vitales, pero de manera global, no se encontraron diferencias significativas en las tasas de crecimiento poblacional estocástico entre regiones. La importancia de los diversos componentes del ciclo vital en las diferencias en las tasas de crecimiento poblacional varió según la escala espacial analizada, aunque el reclutamiento fue la tasa vital con mayor influencia tanto entre regiones como dentro de ellas. Por otra parte, se encontró el mismo patrón de diferenciación demográfica entre poblaciones dentro de las regiones central y periférica: en ambas, se encontró un grupo de poblaciones con contribuciones positivas del crecimiento y el decrecimiento, y contribuciones negativas del reclutamiento y la supervivencia, presentando el resto de poblaciones el patrón contrario. Por último se encontró que, dentro de cada región, el patrón de diferenciación entre poblaciones estaba correlacionado con el régimen de precipitación de las poblaciones, mientras que las diferencias a escala continental se relacionaron con las diferencias en temperatura. Globalmente, nuestros resultados muestran una notable variabilidad entre poblaciones en el ciclo vital de *P. coronopus*, que parece tener un papel relevante en su persistencia en ambientes muy diferentes. Esta flexibilidad demográfica podría explicar el éxito de algunas especies a lo largo de amplias y heterogéneas áreas de distribución.

Capítulo 3

La coexistencia de especies con tamaños de semilla diferentes constituye un tema recurrente de debate en ecología de comunidades, y para explicar este fenómeno en ambientes heterogéneos se ha propuesto recientemente un compromiso (*trade-off*) entre fecundidad y tolerancia al estrés. En este estudio se analiza por primera vez una extensión intraespecífica de este modelo, con el objetivo de evaluar si dicho compromiso también permite entender la variación interpoblacional en la producción de semillas en especies de amplia distribución bajo gradientes de estrés. Recolectamos semillas de 14 poblaciones de *P. coronopus* a lo largo de la costa atlántica en el norte de África y en Europa. Esta planta presenta dimorfismo en las semillas, produciendo semillas basales grandes, con una cubierta mucilaginosa que facilita la absorción de agua (semillas más tolerantes al estrés), y semillas apicales pequeñas que carecen de dicha cubierta (semillas menos tolerantes al estrés). Analizamos la variación entre poblaciones en cuanto a número, tamaño y producción de mucílago de las semillas basales y apicales, e investigamos su posible relación con las condiciones ambientales locales y el tamaño de los individuos. Las poblaciones con mayor estrés (mayor temperatura, menor precipitación y menor materia orgánica en el suelo) produjeron menos semillas por fruto, un mayor predominio de semillas basales respecto a apicales, y semillas basales más grandes y con mayor producción de mucílago. Estos resultados sugieren que un *trade-off* entre fecundidad y tolerancia a nivel de fruto podría explicar la variación en la producción y en las características de las semillas entre las poblaciones de *P. coronopus*. Por otra parte, se encontró que la producción total de semillas a nivel de individuo, con un patrón opuesto a la producción a nivel de fruto, estaba más relacionada con el tamaño de planta y con otros componentes del ciclo vital, como una estrategia adicional de la especie para adaptarse al gradiente ambiental existente a lo largo de su distribución. El modelo de la fecundad-tolerancia podría constituir, bajo gradientes de estrés, un marco ecológico complementario al clásico compromiso entre el número y el tamaño de semillas. Deberían considerarse, no obstante, los diferentes niveles de fecundidad, y diferentes caracteres de las semillas, con el fin de entender las estrategias que presentan las plantas de amplia distribución para optimizar su *fitness* a lo largo de gradientes ambientales.

Capítulo 4

Analizar los patrones y las causas de la variación fenotípica y genotípica dentro de las poblaciones puede ayudar a entender la variabilidad natural presente en las especies, y a predecir sus respuestas a cambios en las condiciones ambientales. En este estudio comparamos la variación fenotípica y la diversidad genética en la especie herbácea de amplia distribución *Plantago coronopus* a lo largo de todo su gradiente latitudinal en Europa, en relación con factores medioambientales y geográficos. La diversidad genética se estimó en 18 poblaciones a partir de marcadores moleculares AFLP (del inglés, *Amplified Fragment Length Polymorphism*), y la variabilidad fenotípica se analizó en un subconjunto de 11 poblaciones, en seis caracteres de relevancia ecológica (tamaño de planta, tasa de crecimiento individual, fecundidad, tamaño de semilla, producción de mucílago y ratio entre dos tipos de semilla). También estimamos la variabilidad local en factores ambientales como la temperatura, la precipitación y la competencia intraespecífica, y consideramos la posición central o periférica de las poblaciones. La variación fenotípica y la diversidad genética no presentaron una correlación significativa dentro de poblaciones a lo largo del rango de distribución. La variación fenotípica se correlacionó, en cambio, con la variabilidad en la precipitación, y la diversidad genética mostró una relación significativa con la posición de las poblaciones, lo que indica que ambos tipos de variación parecen estar modulados por procesos diferentes. El régimen de precipitación parece haber actuado como un agente selectivo para la variación dentro de poblaciones en la mayoría de los caracteres ecológicos, mientras que probablemente algunos procesos demográficos históricos han reducido la diversidad genética neutral en las poblaciones periféricas respecto a las centrales. La correlación positiva entre la variabilidad en la precipitación y la variación fenotípica también sugiere que las poblaciones de especies vegetales podrían desarrollar un mayor potencial adaptativo en ambientes variables respecto a unas condiciones más estables. Nuestro estudio ofrece un criterio adicional a la hora de predecir la futura distribución de las especies ante cambios ambientales.

3. Discusión global y conclusiones

En esta tesis hemos analizado la variación en aspectos demográficos y de *life-history* en la planta herbácea de amplia distribución *Plantago coronopus* durante varios años y a lo largo de gran parte de su rango latitudinal, considerando los efectos de la posición central *vs*. periférica de las poblaciones, los principales factores ambientales y la diversidad genética. Esta aproximación a gran escala espacio-temporal nos ha proporcionado una buena visión de la variación natural presente en esta especie. Además, la combinación de diferentes fuentes de información y el análisis de un amplio rango de componentes del ciclo vital nos han permitido entender los patrones y las causas de dicha variación y testar la validez de algunos modelos ecogeográficos y genéticos.

Las poblaciones de la periferia norte presentaron unas menores tasas de fecundidad (ver Capítulo 1) y una menor diversidad genética (ver Capítulo 4) que las poblaciones centrales. Sin embargo, las poblaciones del norte presentaron una mayor densidad y mayores tasas de reclutamiento, y no difirieron respecto a las poblaciones centrales en cuanto a tasas de crecimiento poblacional estocástico ni en la variabilidad temporal en las tasas vitales (ver Capítulos 1,2). Por lo tanto, nuestro estudio confirma las predicciones clásicas para las poblaciones en la periferia desde un punto de vista genético, pero no desde una perspectiva demográfica. Estas discrepancias muestran los riesgos de utilizar los resultados de un componente de la biología de las especies para inferir patrones en otro componente.

Los factores medioambientales tuvieron una gran influencia en *P. coronopus* tanto en caracteres individuales como en parámetros poblacionales. El tamaño de semilla, por ejemplo, considerado tradicionalmente como un carácter poco variable dentro de las especies, mostró una gran variabilidad entre poblaciones a lo largo del gradiente medioambiental (ver Capítulo 3). En cuanto a parámetros poblacionales, se encontró un mismo patrón de diferenciación demográfica dentro de las regiones central y periférica, en función de las contribuciones de las tasas vitales a las tasas de crecimiento poblacional estocástico, y en respuesta a cambios en el régimen de precipitaciones (ver Capítulo 2). Este resultado sugiere que cada conjunto de condiciones ambientales podría llevar asociadas ciertas estrategias demográficas.

Diversos factores medioambientales analizados, como la temperatura, la competencia intraespecífica o la fertilidad del suelo, tuvieron efectos sobre los individuos y las poblaciones de *P. coronopus*. Sin embargo, la precipitación, tanto en cuanto a valores medios como a variabilidad, parece tener el papel más importante en la variación intraespecífica encontrada en caracteres demográficos y de historia vital. Este efecto parece manifestarse principalmente a través de su influencia en el reclutamiento (ver Capítulo 1). Por una parte, un menor reclutamiento en las poblaciones centrales respecto a las periféricas, debido a una falta de disponibilidad de agua en las dunas, podría haber promovido una serie de cambios en diversos caracteres reproductivos, como una mayor tolerancia de las semillas al estrés hídrico y una mayor producción total de semillas para aumentar las posibilidades de germinación (ver Capítulo 3). Por otra parte, la precipitación también podría afectar a parámetros demográficos, ya que se encontró que el reclutamiento de nuevos individuos tenía una gran influencia en la densidad de plantas adultas (ver Capítulo 1) y en las tasas de crecimiento poblacional estocástico (ver Capítulo 2).

La variación fenotípica dentro de las poblaciones en diversos caracteres vegetativos y reproductivos no mostró una correlación con la diversidad genética, y sí mostró en cambio una correlación con la variabilidad ambiental, sugiriendo un proceso de adaptación selectiva (ver Capítulo 4). La diversidad genética se correlacionó mejor con la posición de las poblaciones dentro del rango de la especie, probablemente como resultado de los procesos demográficos ocurridos en el pasado y que habrían reducido la variación genética en la periferia.

Globalmente, por tanto, las condiciones ambientales parecen tener una mayor influencia en la variación demográfica y de historia vital de *P. coronopus* que la posición de las poblaciones dentro del rango de la especie. De hecho, parece necesario evaluar si las poblaciones que ocupan posiciones geográficas periféricas también experimentan unas condiciones ambientales marginales, ya que numerosos estudios, entre ellos el nuestro, muestran que algunas especies podrían ocupar hábitats favorables incluso en las áreas periféricas de los rangos. En cualquier caso, parece aconsejable testar empíricamente el patrón de cada especie, y analizar para ello el efecto de las condiciones ambientales en un amplio rango de tasas vitales, ya que las condiciones favorables para una determinada tasa vital podrían ser perjudiciales para otra.

Plantago coronopus parece presentar una gran diversidad de mecanismos para adaptarse al marcado gradiente medioambiental existente desde el norte de África hasta el norte de Europa. En primer lugar, presenta un dimorfismo de semillas más acentuado en las poblaciones centrales, de condiciones ambientales más impredecibles, con el objetivo de incrementar las posibilidades de éxito de la descendencia, una estrategia denominada *bet-*

hedging (del inglés, apuesta segura). En segundo lugar, la variabilidad dentro de poblaciones en algunos caracteres vegetativos y reproductivos parece estar correlacionado con el grado de variabilidad en las condiciones ambientales locales. En tercer lugar, *P. coronopus* presenta cambios compensatorios en las diversas tasas vitales que componen su ciclo de vida (fecundidad, crecimiento, supervivencia y reclutamiento). De manera global, nuestro estudio sugiere que la clave del éxito de esta y otras especies de amplia distribución residiría en una gran variabilidad intra- e inter-poblacional en diversos caracteres de relevancia ecológica, y en cambios demográficos a diferentes escalas espaciales.

Finalmente, nuestro estudio deja una serie de campos abiertos para la investigación. Desde un punto de vista filogeográfico, sería interesante analizar el comportamiento de las poblaciones en otras zonas periféricas, al sur y al este del rango de distribución de *P. coronopus*. Asimismo, se podría realizar un análisis más detallado de los procesos de diferenciación genética entre poblaciones a lo largo del rango, y del papel de fenómenos como la plasticidad fenotípica y la adaptación local a la hora de determinar la variación encontrada en esta especie.

Report of the supervisor

Report of the supervisor

Dr. María Begoña García, supervisor of the Doctoral Thesis presented by Jesús Villellas Ariño, certifies that the four studies included in this work have been submitted to international, well recognized journals by the scientific community, with peer review.

The first two chapters have been accepted in two journals that are ranked in the first quartil (Q1) of the "Ecology" category according to the JCR published in 2011. The first one is online since February 2012 in **Ecography,** which has an Impact Factor (IF) of 4.188 (5.54 in the last five years) and it is edited by the Nordic Ecological Society. This journal is positioned as 26th of 133 listed in that category, and 4th out of 37 journals in the "Biodiversity and conservation" category. The second paper was recently accepted by **Ecology**, a journal of long tradition, published by the Ecological Society of America (ESA). It is ranked as 19th out 133 journals (Q1), with an IF of 4.85 (6.01 in the last five years). The third chapter is online since November 2012, in this case in a journal edited by the German Ecological Society: **Plant Biology**, which has an impact factor of 2.40 and is ranked as 54 of 189 journals in the category of "Plant Biology" (Q2). The last study has bee recently submitted (currently under review) to a quite new journal of the ESA family: **Ecosphere**. This online, open-access journal started in 2010, and that is the reason it has not IF yet.

Dr. María Begoña García certifies that all the four studies presented by Jesús Villellas in this Doctoral thesis have been leaded by him under my supervision. In this way, J. Villellas demonstrates full capacity to develop independent and high quality research in the field of Ecology.

Chapter 1.

Villellas, J., J. Ehrlén, J. M. Olesen, R. Braza, and M. B. García (*in press*). Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus*. Ecography, doi: 10.1111/j.1600-0587.2012.07425.x.

Contributions: in this paper, J. Villellas carried out most of the extensive fieldwork required across Europe for 4 years, and was the main responsible for the analysis of the data and the writing of the paper. Coauthors participated in the experimental design (MBG), assisted occasionally with fieldwork (MBG, RB, JMO, JE) and advised with statistical analyses and during manuscript writing (MBG, JE).

Chapter 2.

Villellas, J., W. F. Morris, and M. B. García (*in press*). Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb. Ecology.

Contributions: J. Villellas carried out most of the extensive fieldwork necessary for this the paper, being also the main responsible of statistical and demographic analysis and manuscript redaction. He also participated in the design, whereas couthors helped him during the fieldwork (MBG), data analysis (WFM), and the writing of the paper (WFM, MBG).

Chapter 3.

Villellas, J., and M. B. García (*in press*). The role of the tolerance-fecundity trade-off in maintaining intraspecific seed trait variation in a widespread dimorphic herb. Plant Biology, doi: 10.1111/j.1438-8677.2012.00684.x.

Contributions: the role of J. Villellas in this paper spanned from fieldwork and laboratory measurements, till statistical analysis and writing. MBG participated in the design and advised for data analysis and manuscript writing.

Chapter 4.

Villellas, J., R. Berjano, A. Terrab, and M. B. García (*in review*). Environmental, genetic and geographical correlates of phenotypic variation within populations of a common herb in Europe. Ecosphere.

Contributions: J. Villellas leaded most of the phases of this eco-genetic study. He did fieldwork over years in most populations, participated in the genetic analysis, analysed field data and their correlation with genetics, and wrote the paper. Coauthors helped with experimental design (MBG), fieldwork (MBG), genetic analysis (RB, AT), and advise during writing (MBG, AT).

Besides these four papers, J. Villellas is participating in another manuscript on a related topic of the same studied system, which will be hopefully submitted soon to an international Journal. He will be also co-author of any potential paper using the information gathered over years for *Plantago coronopus*. I finally certify that none of the coauthors has used, in any form, the studies presented here for another Doctoral Thesis.

Zaragoza, January 2013

Mª Begoña García González

Instituto Pirenaico de Ecología (CSIC)

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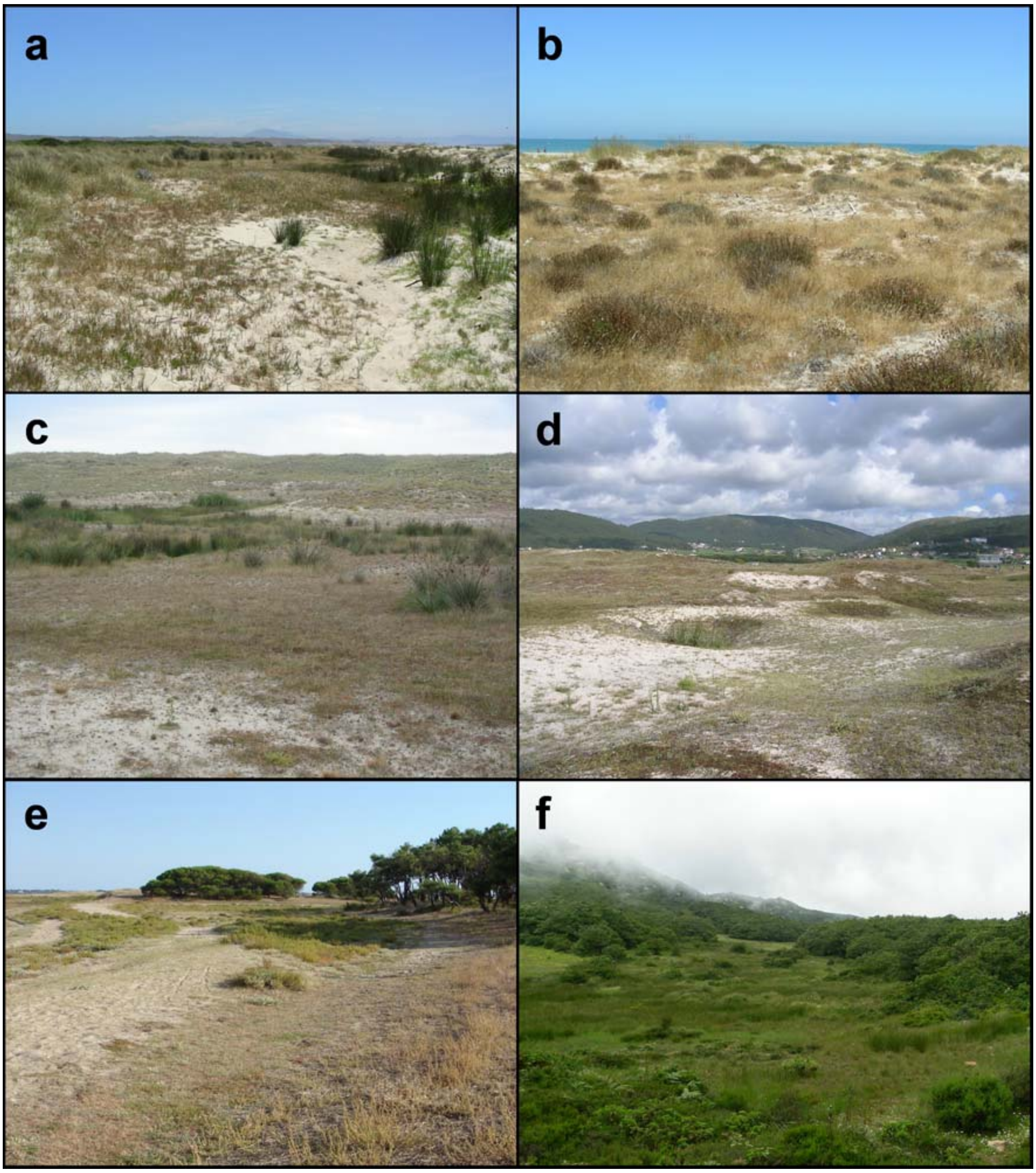
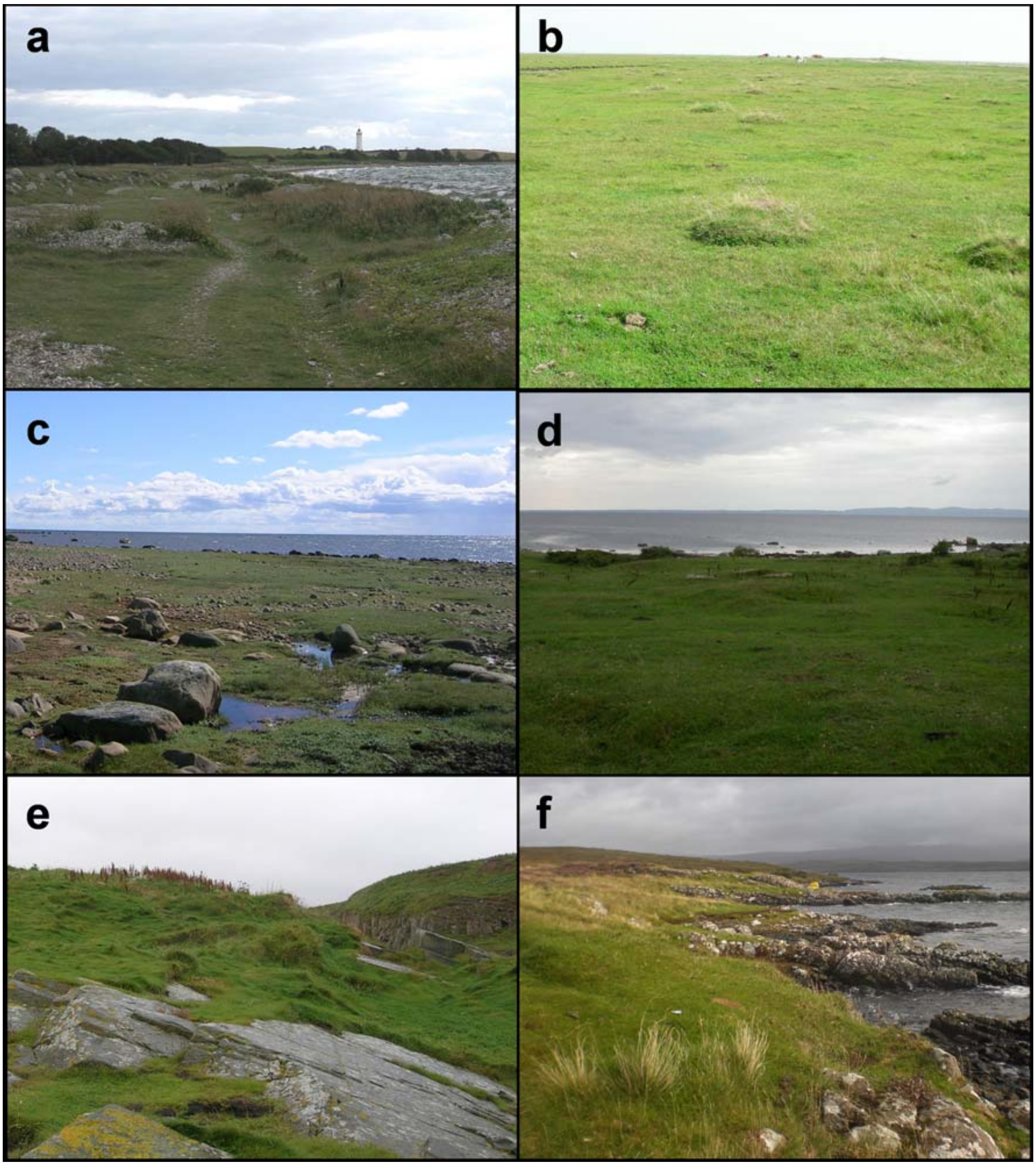
Appendices

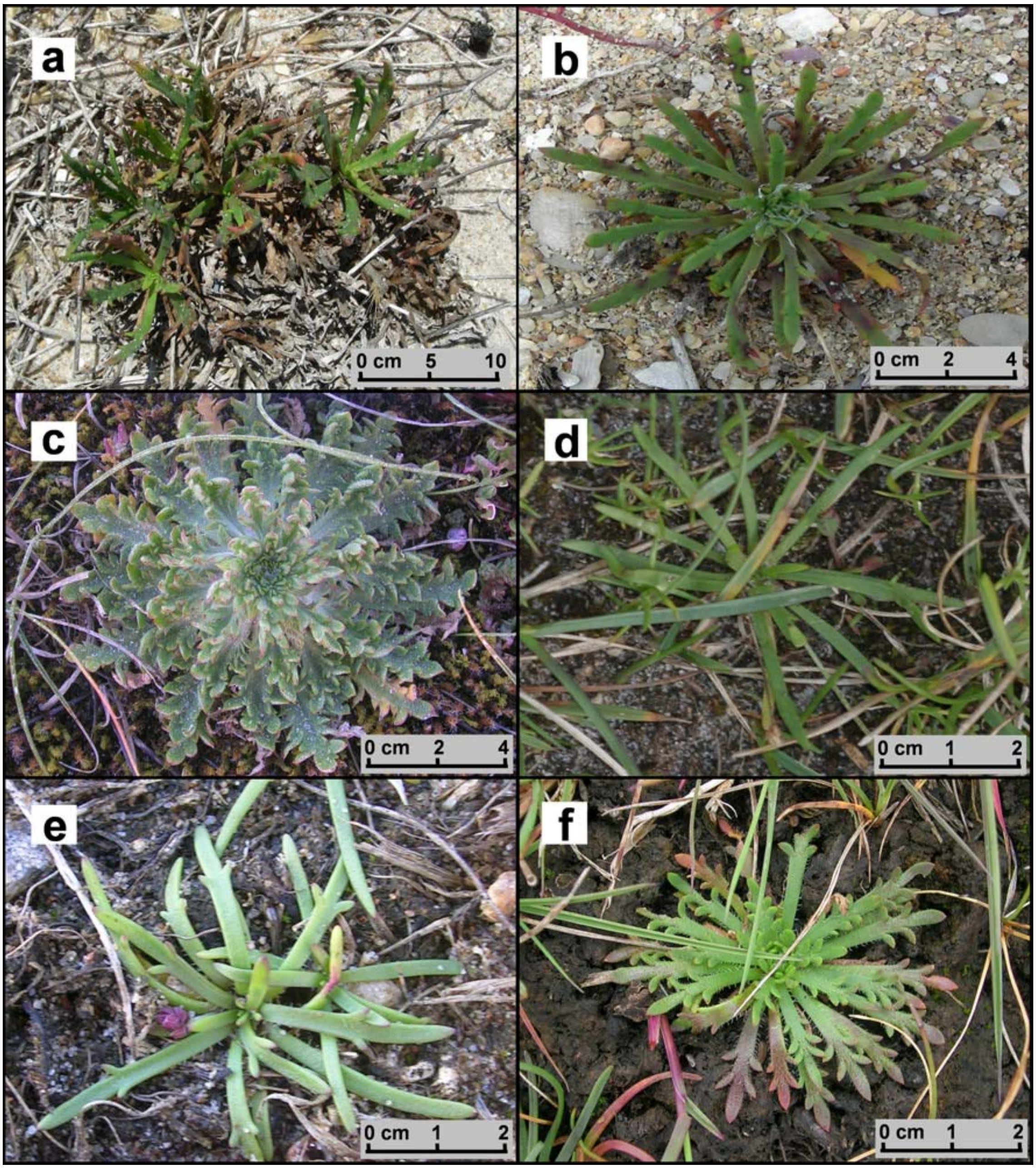
Appendix 1 General view of central populations of *Plantago coronopus* monitored for demographic analyses: a) T (Tarifa, Spain); b) CA (Camposoto, Spain); c) C (Corrubedo, Spain); d) TB (Traba, Spain); e) F (Pen Bron, France); f) BN (Bosque Niebla, Spain; only analyzed in chapter 4).



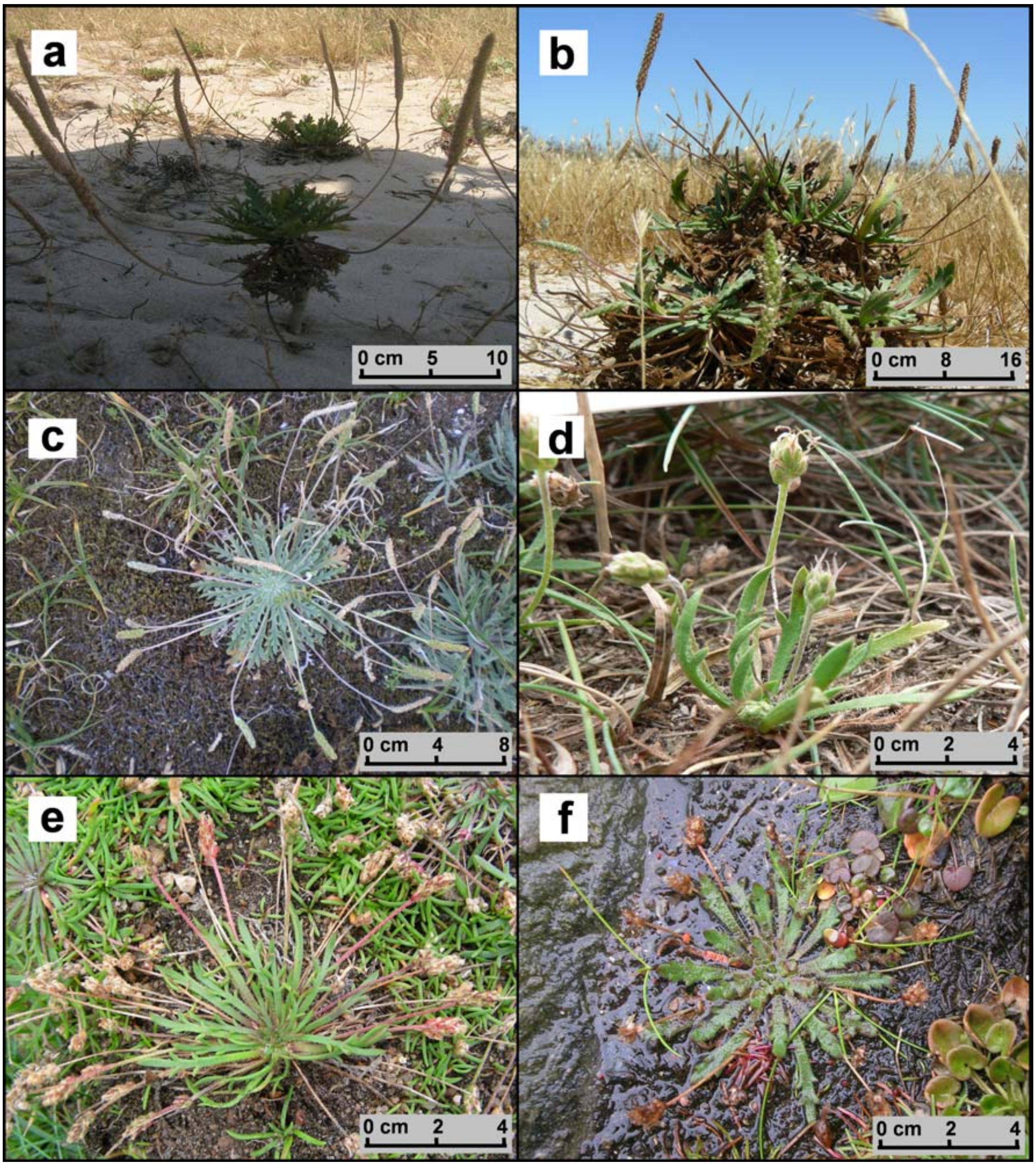
Appendix 2 General view of northern peripheral populations of *Plantago coronopus* monitored for demographic analyses: a) DH (Helnaes, Denmark); b) DS (Skallingen, Denmark); c) SG (Glommen, Sweden); d) ST (Torekov, Sweden); e) EA (Aberdeen, Scotland); f) ES (Skye, Scotland).



Appendix 3 Phenotypic variability among vegetative individuals of central (a, b, c) and northern peripheral (d, e, f) populations of *Plantago coronopus*: a) CA (Camposoto, Spain; plant with several rosettes); b) C (Corrubedo, Spain); c) TB (Traba, Spain); d) DH (Helnaes, Denmark); e) SG (Glommen, Sweden); f) ES (Skye, Scotland). Use the scales for comparing plant size among photographs.



Appendix 4 Phenotypic variability among reproductive individuals of central (a, b, c) and northern peripheral (d, e, f) populations of *Plantago coronopus*: a) T (Tarifa, Spain); b) CA (Camposoto, Spain; plant with several rosettes); c) TB (Traba, Spain); d) SG (Glommen, Sweden); e) ST (Torekov, Sweden); f) EA (Aberdeen, Scotland). Use the scales for comparing plant and inflorescence size among photographs.



Appendix 5 Methodology for this study: a) Plot of 1 m^2 used for demographic monitoring in Tarifa, Spain; b) Plot of 0.25 m^2 used for demographic monitoring in Helnaes, Denmark; c) Linear transect used for calculating population density in Aberdeen, Scotland; d) Soil sample taken from Traba, Spain; e) Material used in the laboratory to handle seeds; f) Placental tissue separating two big basal seeds and one small apical seed of *P. coronopus* in the same fruit; g) Leaves stored in silica gel for genetic analyses; h) Eppendorf tubes with leaf material after being shaken for DNA extraction.