The assembly and disassembly of ecological networks in a changing world

Memoria presentada por:

Miguel Lurgi Rivera

para optar al grado de Doctor

Con el visto bueno de:

Director: Dr. José M. Montoya Terán
Instituto de Ciencias del Mar / CSIC
Centre de Recerca Ecologica i Aplicacions Forestals

Tutor: Bernat Claramunt López
Centre de Recerca Ecologica i Aplicacions Forestals
Departament de Biologia Animal, Biologia Vegetal i Ecologia /
Universitat Autonoma de Barcelona

Programa de Doctorado en Ecologia Terrestre

Centre de Recerca Ecologica i Aplicacions Forestals
Universitat Autonoma de Barcelona

Bellaterra, diciembre de 2013

Universitat Autònoma de Barcelona

CREAF

The assembly and disassembly of ecological networks in a changing world

Ph.D. Thesis

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Bellaterra, diciembre de 2013

Abstract

The assembly, structuring and functioning of natural communities, composed of many species forming complex networks of ecological interactions, has puzzled ecologists for many generations. Early ecological research determined that community size and complexity (measured as connectivity in the network of ecological interactions) limit community stability, and hence impose constraints to communities to become indefinitely complex or speciose.

Community assembly and stability research uncovered the fact that food web architecture is the key to community stability and persistence. Scientists thus started to focus on the understanding of complex networks of interactions between species, and it was soon realised that species population dynamics are influenced by biotic interactions within the overall network. Moreover, certain features observed in the structure of ecological networks are responsible for the maintenance of stability and species persistence in different kinds of ecological communities. The next step in ecological networks research is to incorporate several interaction types into a broader ecological scenario. This will further our knowledge in community structure and stability.

Global change is affecting all ecosystems across the globe, having profound impacts over the delicate balance of nature. It has already caused an unprecedented number of extinctions, and the consequent damage to ecosystem structure and functioning has prompted many to suggest that we are currently witnessing the sixth mass extinction in the history of the Earth. The main big challenge for ecological research that lies ahead is to understand and predict how different components of global change are affecting and will likely affect complex ecosystems.

In this thesis I tackle this challenge following an integrative empirical-theoretical approximation exploring the effects of global change -climatic warming, biodiversity loss and species invasion- on multispecies communities. In addition, I investigate what makes ecological communities stable through their assembly, and how this stability may be affected by global change.

Specifically, I employed a combination of empirical results review and data analysis, a novel conceptual framework for the analysis of relationships between different dimensions of stability, theoretical models grounded on realistic food web structure and ordinary differential equations to simulate populations dynamics, and individual-based spatially explicit models with a mixture of ecological interaction types in order to gain predictive insights on the effects of different components of global change on natural communities and several factors behind the stability of these assemblages of species.

Some of my key findings are: (1) Species range shifts triggered by climate change are generating novel communities. These are characterized by consistent novel patterns where body size distributions within the food webs are getting shifted towards smaller sizes, specialised interactions are getting lost, and interaction strengths are getting stronger in general, with further consequences for community dynamics. (2) Different dimensions of ecological stability are correlated in non-trivial ways. Biodiversity loss leads to a decoupling of the correlations previously observed between stability measures. This leads to highly unpredictable dynamics of ecological communities after major disturbances. (3) When focusing on biological invasions I find that food web structure is a strong determinant of invasion success. Less connected, more modular, and more heterogeneous communities in terms of diet breadth are more robust to biological invasions. Invasions make communities more connected and less modular in general, rendering them even more fragile to invasions. Species traits of the invasive species, such as body size and the ability to capture prey, are also strong determinants of invasion success. (4)

Finally, mutualistic interactions increase both temporal stability and spatial stability, by keeping spatial aggregation more constant. Distributions of interaction strengths across the entire ecological network are shifted towards lower values as mutualism increases.

Resumen

El ensamblaje, estructuración y funcionamiento de las comunidades naturales, compuestas de muchas especies que forman redes complejas de interacciones ecológicas, ha desconcertado a los ecólogos durante muchas generaciones. Investigación ecológica pionera determinó que el tamaño de la comunidad y su complejidad (medida como la conectividad en la red de interacciones ecológicas) limita la estabilidad de la comunidad, y por lo tanto impiden que las comunidades sean indefinidamente complejas o ricas en especies.

Investigación sobre el ensamblaje y la estabilidad en comunidades naturales ha descubierto que la arquitectura de la red trófica es la clave para la estabilidad de la comunidad y su persistencia. Así, los científicos comenzaron a centrarse en la comprensión de las complejas redes de interacciones entre especies, y pronto se dieron cuenta de que la dinámica de las poblaciones de las comunidades naturales se rigen por la estructura de estas redes. Por otra parte, ciertas características observadas en la estructura de las redes ecológicas son responsables del mantenimiento de la estabilidad en diferentes tipos de comunidades ecológicas. El siguiente paso en la investigación de las redes ecológicas es incorporar varios tipos de interacción en un escenario ecológico más amplio. Esto incrementará el conocimiento de la estructura y la estabilidad de la comunidad.

El cambio global está afectando los ecosistemas de todo el mundo, con profundos impactos sobre el delicado equilibrio de la naturaleza. Ya ha causado un número sin precedentes de extinciones, y el consiguiente daño en la estructura y funcionamiento del ecosistema ha llevado a muchos a sugerir que en estos momentos estamos presenciando la sexta extinción masiva en la historia de la Tierra. El principal desafío para la investigación ecológica que tenemos por delante es entender y predecir cómo el cambio global está afectando, y es probable que afecte en el futuro, los ecosistemas complejos.

En esta tesis enfrento este desafío utilizando una aproximación empírico-teórica integradora para explorar los efectos del cambio global -cambio climático, pérdida de biodiversidad e invasión de especies- en comunidades compuestas por múltiples especies. Adicionalmente, investigo qué hace que las comunidades ecológicas sean estables durante su ensamblaje, y cómo esta estabilidad puede verse afectada por el cambio global.

En concreto, he empleado una combinación de revisión de resultados y análisis de datos empíricos, un novedoso marco conceptual para el análisis de las relaciones entre diferentes dimensiones de la estabilidad ecológica, modelos teóricos fundamentados en redes tróficas con estructuras realista y ecuaciones diferenciales ordinarias para simular la dinámica de las poblaciones, y modelos espacialmente explícitos basados en el individuo con una mezcla de tipos de interacciones ecológicas; con el fin de obtener una visión predictiva de los efectos de los diferentes componentes del cambio global sobre las comunidades naturales y sobre los factores que explican la estabilidad de estos conjuntos de especies.

Algunos de mis principales hallazgos son: (1) cambios de distribuciones de especies provocados por el cambio climático están generando comunidades nuevas. Estas últimas se caracterizan por nuevos patrones en que las distribuciones de tamaño corporal dentro de las redes tróficas se están desplazando hacia tamaños más pequeños, las interacciones especialistas se están perdiendo, y las fuerzas de interacción son cada vez más fuertes en general, con consecuencias importantes para la dinámica de la comunidad. (2) Las diferentes dimensiones de la estabilidad ecológica se correlacionan de manera no trivial. La pérdida de biodiversidad lleva a un desacoplamiento de estas correlaciones. Esto conduce a dinámicas altamente impredeci-

bles en comunidades ecológicas sujetas a perturbaciones. (3) Enfocándonos en las invasiones biológicas vemos que la estructura de la red trófica es un factor determinante para éxito de la invasión. Comunidades menos conectadas, más modulares, y más heterogéneas en términos de amplitud de la dieta de las especies que las componen son más robustas a las invasiones biológicas. Las invasiones hacen a las comunidades más conectadas y menos modulares en general, lo que las hace aún más frágiles a las invasiones. Algunos rasgos de las especies invasoras, como su tamaño corporal y su capacidad de capturar la presa, también son fuertes determinantes del éxito de la invasión. (4) Por último, las interacciones mutualistas incrementan tanto la estabilidad temporal como la estabilidad espacial, mediante el mantenimiento de una agregación espacial más constante. Las distribuciones de las fuerzas de interacción en la red se desplazan hacia valores más bajos a medida que la fracción de mutualismos en la comunidad aumenta.

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Acknowledgements

I would like to take this opporunity to remember my family for all the support during all these years. None of this would have been possible without them. Especially my daughter, for making my life joyful, fun, worth living... and most of all for teaching me the value of life and happiness.

My friend and scientific teacher, José (Montoya) has been a strong influence on my ecological thinking. Together, we came up with the most exciting and fullfilling ideas. I hope we can continue walking this scientific path together for many years to come.

This PhD thesis was funded by Microsoft Research through its PhD Scholarship Programme.

Introduction

The assembly, structuring and functioning of natural communities, composed of many species forming complex networks of ecological interactions, has puzzled ecologists for many generations. It is one of the main unresolved mysteries of our world, one that could be paired with other important phenomena studied by the sciences such as what are the causes behind dynamical changes in weather patterns, what are the regimes followed by earthquakes on our planet, how our immune system is able to produce resistance against numerous pathogens, the formation and development of an embryo, how the brain works, or how was life formed.

All these phenomena have one fundamental common feature: they are produced through emergent behaviour of complex systems made up of simpler interacting entities. They have been possible only through laws acting around us. All this complexity and how it arises in these disparate systems brings with itself a suite of universal properties that make the organisation of these systems even more mysterious. They are subject to uncertainty that in turn make their dynamics highly dependant and sensitive to the initial conditions from which one starts looking at them, a feature associated with the so-called chaos.

In 1963, meteorologist Edward Lorenz, looking at non-linear models for weather forecasting based on atmospheric phenomena, realised that "*two states differing by imperceptible amounts may eventually evolve into two considerably different states... an acceptable prediction of an instantaneous state in the distant future may well be impossible...*" [140]. Based on these and other observations, he later coined the term 'butterfly effect' laying the foundations of chaos theory (figure 1). Since the early realisation in the realm of statistical physics, that chaos was ubiquitous in the natural world; scientists have sought to understand physical phenomena from a new perspective. They had to embrace the fact that **some systems, even the simplest ones they could think of that followed deterministic rules, could display chaotic behaviour. This is the key to chaos: it is deterministic**. This phenomenon is present in our everyday lives and is the reason why so many things are organised the way they are. Complex systems live at the edge of chaos. Complexity builds up until it reaches a point in which a further increase on it, like an additional entity in the network of interactions, an additional interaction in the set of all possible ones, or one more individual within a population, might tip the balance towards chaotic dynamics or to alternative stable states. Physicists call this phenomenon self-organised criticality (SOC).

Self-organised criticality turns out to be present at multiple levels of biological organisation. From gene regulatory networks in which even a small mutation can cause dramatic effects on the phenotype of an individual, through small changes in molecular metabolic pathways that can cause lethal diseases, all the way up to complex ecosystems formed of many species, in which the effect of a species extinction, or even a small change in the abundances of a given species population, can ripple throughout the entire ecological network and trigger a chain of unanticipated effects on numerous species in the ecosystem. A key aspect of SOC

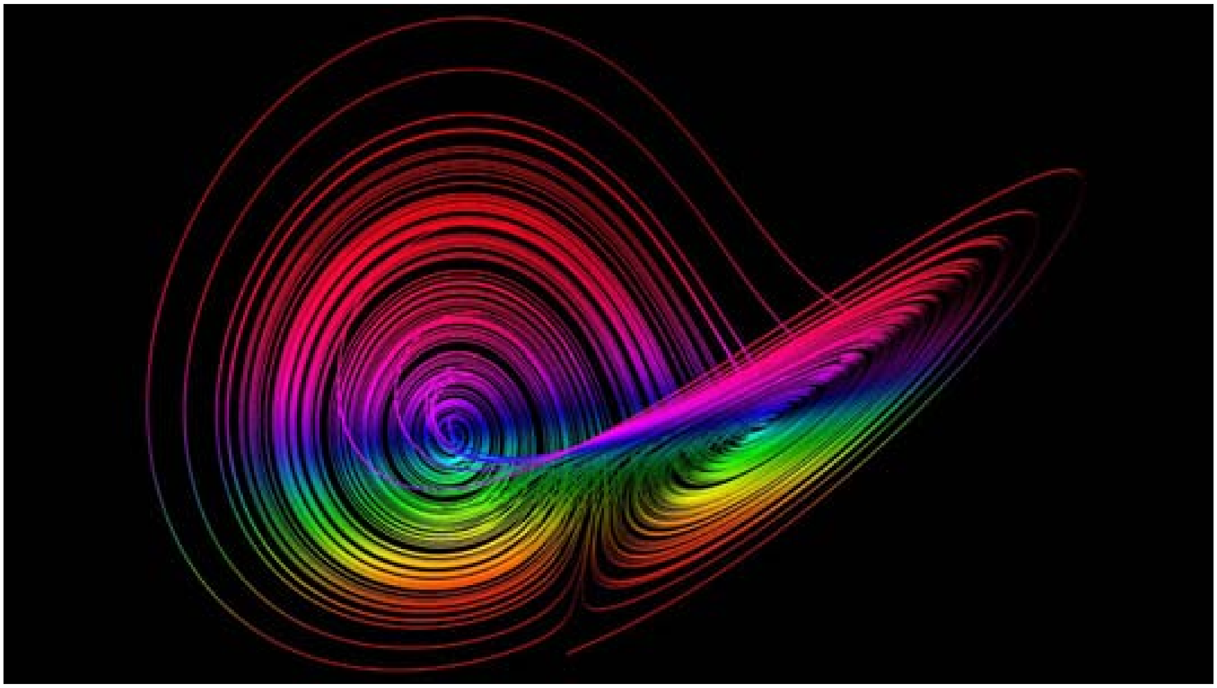


Figure 1: Graphical representation of a Lorenz attractor. A set of deterministic equations is able to display this non-periodic behaviour. This behaviour prompted Lorenz to suggest that any acceptable prediction of the future may well be impossible. Coincidentally the behaviour if this system of equations, when plotted, displays the shape of a butterfly. Lorenz coined the term ‘butterfly effect’ to imply that the flutter of a butterfly could trigger a storm in the opposite part of the world.

is that the events causing these major disruptions are essentially of the same nature of the ones that drove the development of the system. These major disruptions cause the system to either collapse and go extinct, or to achieve one of, possibly several, alternative stable states. Changes among these alternative stable states are known as phase transitions, and SOC is the reason why they are so common in nature.

Complexity and stability in natural ecosystems

The fascinating complexity of the natural world was recognised early in the history of mankind. However, it was not until the publication, by Charles Darwin in 1859, of ‘*On the Origin of the Species*’ that it was acknowledged that this organisation was not only bewildering on its own, but also that it had important implications for our understanding of the biological world. Darwin was able to beautifully summarise the incredibly complex organisation of ecological interactions and its relevance for the understanding of the natural world in his closing remark of ‘*The Origin*’:

> “*It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us (...) There is grandeur in this view of life, with its several powers, having been originally breathed into a few*

> *forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.*"

Figure 2: The bewildering complexity of the trophic interactions in nature is well portrayed by this engraving by Pieter van der Heyden, entitled: *Big Fish Eat Little Fish*.

Ever since Darwin, ecologists have sought to understand what are the fundamental first principles behind the assembly and organisation of these entangled ecological communities (figure 2). Earlier efforts on this direction were mainly due to Charles S. Elton, G. Evelyn Hutchinson, Ramon Margalef, or Robert MacArthur, who in the 1950's started to look at several aspects of community composition and to ask questions like: *why are there so many species in the world?* or *how can they live all together?* In his seminal work '*Homage to Santa Rosalia*' [104], published in 1959, Hutchinson suggested interesting hypotheses about the ultimate causes of biodiversity. In particular, he proposed for the first time the concept of an ecological niche as the fundamental explanation for the existence of so many species. The publication in 1958 of '*The Ecology of Invasions by Animals and Plants*' by Elton was a milestone in the study of ecology that marked the beginning of the study of ecological invasions as an established discipline within ecology. **Perhaps more important from a theoretical angle, Elton laid the basis for the study of community assembly due to the gradual inclusion of species into broader communities**.

However, communities cannot incorporate species indefinitely. Moreover, many species that try to invade communities might not be able to survive and will fail in their attempts to do so. **One of the reasons why this might happen are the fluctuations of the populations of species already present in the community, affecting the ability of alien species to persist**. Thinking along these lines, MacArthur, in 1955, introduced the idea of populations' fluctuations and its relationship with ecological stability [146]. MacArthur argued that the intricacy of the interactions between species in the community was an important determinant of its stability, and hence, of its ability to incorporate new species. In the following years this idea turned out to be fundamental for the study of community assembly and stability. The assembly of ecological communities seemed to be driven by the arrival of species and their ability to survive in the community given their ecological interactions with other species.

The notion of community stability being linked to the complexity of the network of ecological interactions amongst its constituent species was appealing, but very difficult to both formalise theoretically and test empirically. It was not until theoretical studies on local stability analysis on competitive communities and food webs were carried on that earlier hypotheses could be rigorously proved. **In the 70's, Robert May pioneered the theoretical exploration of the relationship between ecological complexity and community stability**. His interests were focused on the effects of complexity, in terms of species richness and connectivity among the species, on community stability. His idea of applying the framework of local stability analysis that had been applied before to study other kinds of complex systems [85], turned out to be the most influential idea in the study of stability in ecological communities [149]. May found that more complex ecosystems (in terms of more species and larger connectivity) were so unstable that they tend to collapse, making their existence statistically improbable (figure 3).

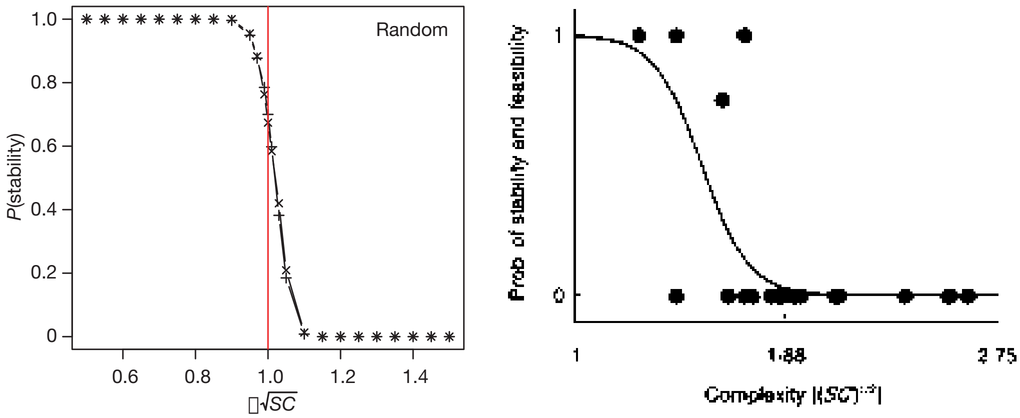


Figure 3: Phase transition observed in the probability of stability of model (plot on the left, taken from [3]) and real (plot on right, taken from [82]) complex communities. As the stability criterion used by May [149] increases, the community approaches a zone in which stability is no longer achievable.

Since then, the majority of the studies of stability on complex connected communities have focused on this type of stability analysis. An exception to this came as early as 1974, when Richard Levins in his seminal work [130], and realising that previous studies on local stability analysis of complex communities, including May's work, were based on competitive communities only, analysed the role of feedback loops on community stability. He found that certain loops configurations where able to confer stability to systems of equal size and connectivity but lacking those feedback loops.

But feedback loops were not the whole story, even after including them into community stability analysis; it was observed that the majority of communities were unable to persist. This was in disagreement with observations of natural systems, in which a myriad of species embarking upon a myriad of different interactions are able to persist. The big challenge then identified by May was to find out the '**devious strategies**', as he called them, by which nature is able to violate this rule [150]; **the workarounds that a natural system has to increase its species and connectivity capacity without sacrificing its stability and persistence**.

The role of predator-prey dynamics

The study of predator-prey interactions dates back to even before modern ecologists had started to ask questions about how complex assemblages of species were possible. Models of predator-prey dynamics as a way of analysing the drivers of fluctuations observed in the dynamics of populations of interacting species had been proposed as early as the 1920's by Alfred J. Lotka and Vito Volterra [141, 265]. Following models proposed for the simulation of dynamics of chemical reactions, based on the transformation of species of molecules into new ones and the consumption of others, these models were able to successfully recreate the dynamics of predators and prey occurring in wild populations. Thus, Lotka and Volterra, independently, developed what has come to be known as the Lotka-Volterra (L-V) population dynamics model, grounded on the solution of ordinary differential equations. The L-V model has been the most widely used model in ecology to simulate the dynamics of biological species interacting via trophic relationships [16, 87]. The model however, was not able to reproduce all predator-prey dynamics observed in nature. One ecologist to realise this was C.S. Holling, who in 1959 extended the L-V dynamical model to include other kinds of functional responses beyond the purely linear one [101] of predator intake over prey abundance. This extension of the model was meant to incorporate the effects of different types of biological phenomena observed in predator-prey interactions into its dynamics, in order to endow it with greater realism. Since then an array of variations to the original L-V model have been developed, according to the necessities of each modelling exercise.

The 80's witnessed a steady rise of studies in community assembly, stability and food web architecture, and how all these processes are related to each other. Most importantly, more realistic food web structures were used. Theoretical ecologists aimed at understanding how the organisation and strength of interactions in food webs would affect the assembly process and the stability of ecological communities. In order to do this, they started to use L-V type models incorporating realistic Holling type functional responses to simulate the dynamics of populations in complex communities. The independent works by Stuart Pimm and John Lawton, and Peter Yodzis on community structure and its implications for stability were a major step towards the integration of food web structure into community stability analysis [205, 201, 281, 282].

Yodzis realised that the connectance of real ecosystems was very different from that used in previous studies on community stability [281]. After introducing realistic food web structures for the first time into local stability analyses of ecological communities, he concluded that stability was very much related to the interacting patterns displayed by natural food webs [282]. He also started thinking about the role of predator-prey interaction strength on community stability [282]. **Pimm and Lawton, on the other hand, were interested in finer-grained aspects of food web organisation**, and they studied particular modules within food webs (such as omnivorous loops), using L-V functional responses, to look at how this **mid-level structural organisation of the food webs affected different types of community stability** [205, 207]. Apart from proposing new ways of calculating community stability, and how to look at it from different angles related to food web complexity [202], Pimm also focused his attention on community assembly, and developed dynamical models with gradual add up of species to look at the process of community assembly. He found that, as suspected by McArthur and Elton 35 years before, more complex communities, both in terms of species richness and number of trophic links between those species, were harder to invade by incoming species [203]. In other words, more complex communities were more resistant to the addition of new species.

A mechanistic understanding of food web organisation

After realising the potential importance of the role of energy flow across food chains for food web dynamics and hence, for stability, Yodzis paired up with Stuart Innes and together developed a bio-energetic version of the L-V model [283]. This model aimed at incorporating two fundamental species traits as central to model species feeding interactions and population dynamics: body size, and metabolic type. This bio-energetic model demonstrated that these species traits might be important for understanding the dynamics of interacting populations and the stability of communities. Soon, it would come to be the foundation of the contemporary modelling approaches for population dynamics, one in which species traits are fundamental to understand ecological organisation.

Another line of research pursued by ecologists at that time, more related to the causes of food web structure rather than its dynamical consequences, was the quest for a mechanistic understanding of food web organisation. Around the 90's, Joel Cohen worked on niche ideas similar to those proposed by Hutchinson 3 decades earlier. **Cohen introduced the concept of the niche of ecological interactions as a main driver behind food web structure**. He envisioned food webs as networks in which trophic interactions occurred between species arranged in a one-dimensional niche. Predators on this niche could only feed on species below them. He proposed the cascade model [51] as a way of generating realistic food web structures following this simple niche rule. Even when the cascade model turned out not to be able to reproduce some of the important features observed in food webs [207], the model served as a good starting point to think about the mechanisms behind food web structure.

These early theoretical studies, both in terms of food web structure and community stability, paved the way for, among other research avenues, two main streams of research in food webs: the search for universal patterns within the architecture of ecological networks, and the search for the mechanistic basis behind the emergence of these patterns and their implications for community stability.

Twenty years had lapsed since May's crucial finding, and even though a lot of progress had been made, some of the devious strategies' that May thought must be behind the organisation of complex ecosystems had yet to be discovered. In the early 90's, and thanks to the legacy of previous research, food web ecologists were thinking about the role of the strength of trophic interactions on the stability of complex communities. Previous theoretical studies had suggested, based on May's model and the realisation that, in addition to species richness and food web connectance, the other key ingredient was the strength of the interactions between species, that the latter could hold the key to ecosystem stability [281]. Ecologists started searching for empirical data to give support to these hypotheses and indeed they found that stability in natural communities was intimately linked to the patterning of interaction strengths across the food web [58]. However, that was not the entire picture; other biologically plausible mechanisms were also found to confer complex interconnected communities with stability. Adaptive foraging, for example, was found to be a stabilising factor in theoretical models of complex communities [125] by allowing predators to switch prey as they became readily available, effectively changing the structure of the realised network and the strengths of its interactions dynamically. Many 'devious strategies' were shown to be at nature's disposal to facilitate the emergence of stability in natural communities, some of which were linked to species traits.

Ecological complexity and stability revisited

Around the same time **-between the 90's and the 00's-, researchers had started to look at other kind of complex systems of interconnected entities in the biological and technological world** (figure 4). Very complex interconnected systems turned out to be more common than previously thought, and scientists looking at them were interested in finding what made them special. Physicists came up with the idea of applying a long-standing, well-established, mathematical tool for understanding collections of interconnected entities to the study of the structure of these complex systems. They imagined entities composing these complex systems as nodes and their interactions as links between these nodes. This is how graph theory met complex systems. It has been a fruitful approximation to the understanding of complex structures as diverse as interconnected web pages on the Internet, your network of friendships, or networks of electrical stations delivering electricity to your house [246, 176]. They have also been found at the most disparate levels of biological organisation, from gene regulatory networks, through networks of molecular reactions forming metabolic pathways, interacting organs forming a living organism, all the way up to species interacting in ecosystems.

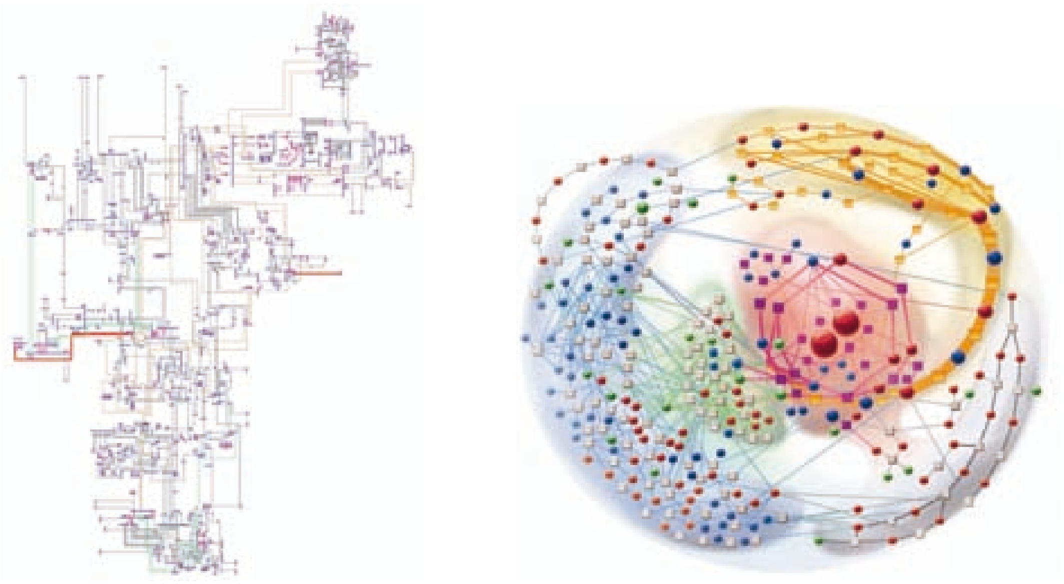


Figure 4: Map of an electric power grid (on the left) -figure taken from [246]-, and graphical representation of the metabolic network of Escherichia coli (on the right) -figure taken from [120]-. These networks are clear examples of the bewildering complexity observed in the natural and technological world.

Some scientists realised that **this way of thinking about complex interconnected systems of similar entities could also be applied to the investigation of ecological networks of interactions between living species**. It allowed them to delve deeper into the structural patterns that, as it was clear by then, characterised natural assemblages of ecological species. In the search for universal patterns in the way species interact, this new perspective turned out to be a big revolution in the study of ecological networks [238, 164, 71, 112]. The extent of its influence was such that soon enough, ecologists realised that universal patterns across networks of ecological interactions could be found in this way not only in food webs [69], but also in mutualistic [12], and even host-parasitoid [158] networks of ecological interactions (reviewed in [162]).

One of the main insights yielded from a complex network approximation to ecological networks was the realisation that these webs displayed characteristic shapes in their degree distributions (the probability distribution describing the frequency of species with a given number of links) [165, 162]. Although this pattern was similar to that found in other types of networks such as the Internet, electric power grids, or social networks, which usually display power-law degree distributions [246]; ecological networks are organised in a slightly different way, with exponential or truncated power-law degree distributions (figure 5). Additionally, food webs were observed to be more clustered than expected by chance [164]: any two species in the food web are only a few links away from each other. **Together, these features are known as small-world properties [246], and they have important implications for the spread of disturbances across the network of interactions**.

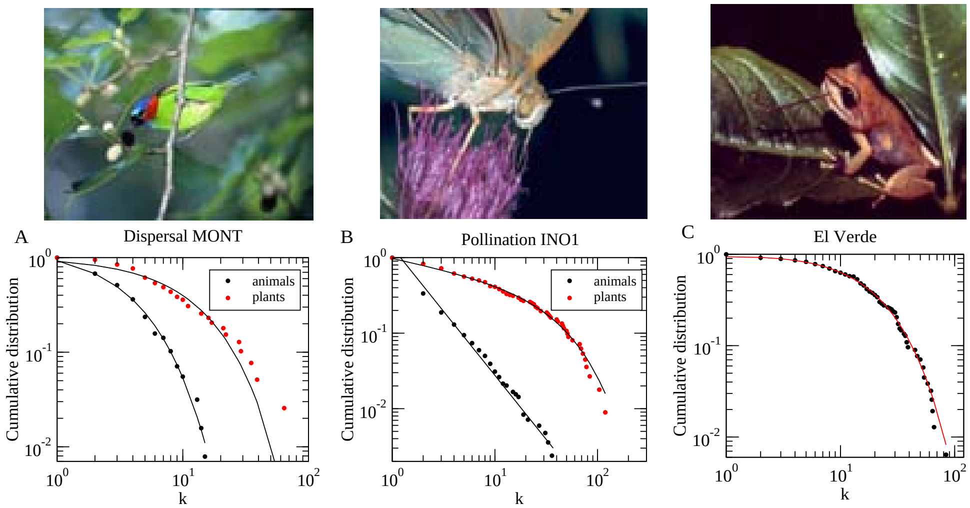


Figure 5: Characterisctic degree distributions observed in different types of ecological networks. In the plots, k is node degree and Pc(k) is the cumulative probability for ≥ k, where P(k) is the probability a species has k links to other species in the network. Fits to the distributions are exponential, truncated power-law, and power-law. Figure provided by José M. Montoya.

This big revolution pervaded the way scientists looked at ecosystems and the way species interact in complex ecological aggregates. It was thus a natural step to think about the role of the special arrangement of interactions within an ecological network on the stability of the community. Research on ecological networks was thus driven towards the role of structural patterns of the network of ecological interactions on the stability of ecosystems. The organisation of links within the network turned out to be important for the stability not only of food webs (e.g. [224]) but also for other types of ecological networks such as plant-animal mutualistic interactions (e.g. [186, 14]). Fundamental similarities were found between these two types of ecological networks such as the asymmetry in their interactions [58, 13, 259]; but also fundamental differences were apparent, like the organisation of links into compartments in food webs [206, 91] vs. a nested architecture in mutualistic networks [12].

All these features observed in the structure of ecological networks have turned out to be important for the maintenance of stability in each type of community [249, 3]. **Compartmentalised architectures confer stability to food webs while nested architectures are responsible for stability in mutualistic networks** [249]. This new way of looking at ecological networks brought new, interesting questions about the mechanisms behind this exquisite organisation. Several mechanisms arose as potential explanations. For example, body size and foraging behaviour were demonstrated to be plausible predictors of food web structure in theoretical models [199], while empirical evidence was found in favour of the potential of body size in structuring complex food webs [278]. **Body size, as these studies demonstrated, has been identified as a strong candidate governing the mechanisms by which the niche of ecological interactions, which Cohen was thinking about 15 years before, is determined**.

These mechanistic explanations were complemented by phenomenological approaches meant to improve the insights offered by niche thinking through the 'cascade' model. In 2000, the niche model was proposed [272], as an improvement of the cascade model, yielding some intuition over the fact that species on an hypothetical niche axis could feed not only on species below them (as suggested by the cascade model), but also on themselves (cannibalism) and on species above them. This relaxation of the model turned out to be successful, and to generate network architectures closer to those observed in natural food webs. This stimulated researchers to envision how other mechanisms could affect the wiring process of the food webs, and to propose new models that incorporate these observations. For example, ideas on how phylogenetic constraints and adaptation would affect wiring patterns in food webs were incorporated into the 'nested-hierarchy' model [47], which yielded a better approximation to the architecture of food webs observed in nature. Since then, further modifications have been done over the 'niche' and the 'nested-hierarchy' models, in the hope of revealing the true mechanisms behind food web organisation.

An important outcome of this revolution in ecological thinking and food webs was the revival of the long-standing complexity-stability debate [151], which since the time of May [150] had occupied the minds of many food web ecologists. With this new knowledge at their disposal, ecologists could now dig deeper into the consequences of including structure into an otherwise random model and extending May's findings into communities with more realistic arrangements of links [3]. Another important advance facilitated by this new way of looking at ecological networks was the extension of studies on community stability, which until then had mainly focused on trophic interactions as the main drivers of population dynamics in natural communities, to other types of ecological networks such as mutualistic ones [186, 14]. Additionally, studies on food webs revealed that their structure was also key to understand not only community stability, but also the consequences of biodiversity loss [238, 72], and other types of disturbances [166] on their structure and dynamics. The field of ecological networks, which was just flowering, was rapidly expanding and providing fresh insights into several areas of ecological research.

Research on ecological networks is now moving towards an even more holistic approach to the study of natural communities. **It has been recognised that natural communities are highly diverse not only in terms of species composition but also in their diversity of interaction types**. Recent research effort has been thus directed towards the incorporation of several interaction types into the same ecological network in order to construct 'networks of networks' that would cover under the same umbrella trophic, mutualistic, parasitic and other types of ecological interactions [189, 79]. Theoretical research has suggested that the mixture of interaction types, and the contribution of each component of the broader ecological network, could be the missing ingredient for the understanding of stability in ecological networks [156, 249, 172]. The combination of interaction types under an unified ecological network could hold the key not only to the stability of natural communities, but also to the understanding of their response to perturbations, which are becoming increasingly common everyday due to the impacts of global change on the Earth's ecosystems.

Global change and ecological networks

Global change is affecting all ecosystems across the globe, having profound impacts over the delicate balance of nature. It has already caused an unprecedented number of extinctions, and the consequent damage to ecosystem structure and functioning has prompted many authors to suggest that we are currently witnessing the sixth mass extinction in the history of the Earth [129, 9]. **Our time is reaching the same levels of previous mass extinctions in three main respects: the magnitude of the change (number of species lost), selectivity of the species that are lost (e.g. bigger species are being lost faster than smaller ones) and the combined, synergistic nature of the causes of extinctions leading to a perfect storm phenomenom** [9]. This sixth mass extinction is not only affecting species but also, as Janzen had already observed in 1974 [108], another kind of extinction, one that "*escapes the eye... a much more insidious kind of extinction: the extinction of ecological interactions*".

These observations suggest that we are now entering a new geological era in the history of the Earth, the Anthropocene, in which a change in the stability in the biosphere is occurring due to human impact. Human action is provoking a phase transition from a previous stable state that has lasted on Earth for the past 10,000 years (the Holocene) to a new alternative state in which not only the balance of species compositions in ecosystems will be affected, but also other geological factors of the Earth such as the chemical composition of the atmosphere and the lithosphere. This has prompted scientists to look for evidence in ecosystems across the globe for these transitional changes, and have suggested that the Earth is approaching a state shift in biodiversity [10]. **The Earth is approaching planetary limits in terms of biodiversity and ecosystem functions loss that once crossed are likely to be impossible to go back over it and recover the previous state** [221] (figure 6). The Earth will then go through a phase transition into a new state, probably very different to anything like the Earth as we know it.

These changes are however fundamentally different from the phenomena that we observe when systems achieve SOC. They are not related to the progressive accumulation of tiny events that are similar in essence to the construction process of the system. They obey different laws and hence, even though they may push the system into a phase transition, they are from a completely different nature than the changes previously experienced by it (e.g. background extinctions are mostly random while current extinctions are highly selective, both in terms of species traits and phylogenetic signal). Additionally, these perturbations are usually much bigger in magnitude than what the system is capable of coping with. **Another feature of global change that sets it apart from the traditional causes of phase transitions is the fact that it has several components. Multiple stressors act in tandem on ecosystems: habitat loss and fragmentation, climatic warming, biological invasions**. Even though the ultimate cause of all of them is human action, they are distinct from each other and together they create a 'cocktail' of causations that have the potential to facilitate the occurrence of a 'perfect storm' over the Earth's ecosystems. **This perfect storm of disturbances has the potential to cause even more non-linear changes in comparison to those that complex ecosystems are constantly subject to, making predictions of any kind increasingly difficult**. In order to be able to make predictions about how the Earth and its constituent ecosystems will change under the current global change scenario, we need to understand the effects of all these stressors on ecosystems -including their synergistic effects-, how this will affect the way these ecosystems go through new kinds of phase transitions, and whether they will achieve alternative stable state like self-organised critical systems sometimes do.

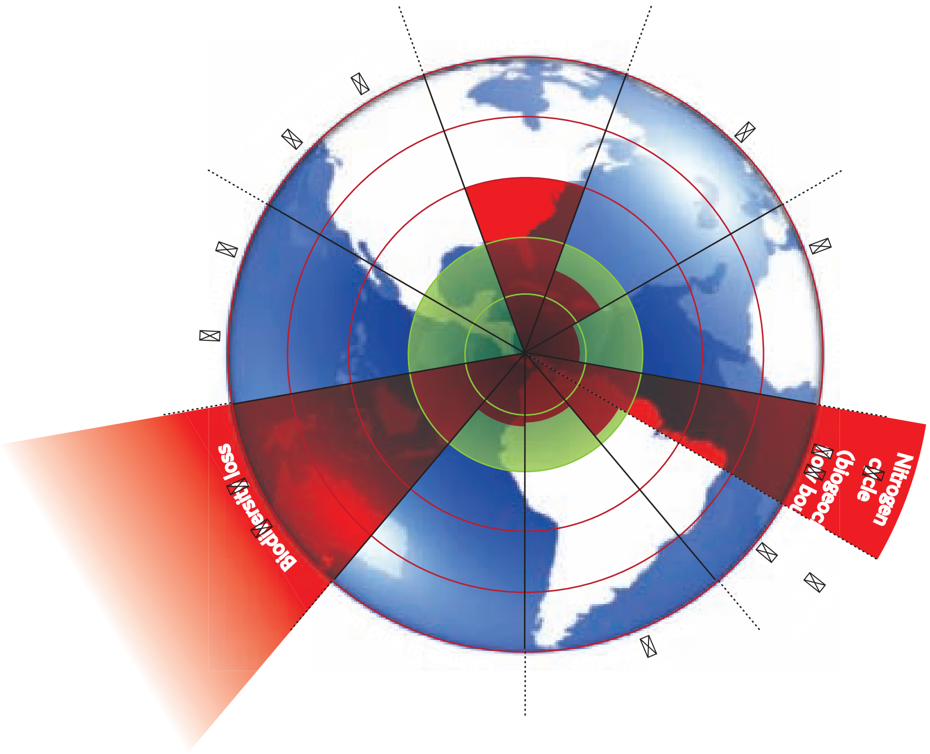


Figure 6: Boundaries for nine planetary systems, three of which have already been exceeded, making going back into a previous state in the Earth safe operating space very difficult. See [221] for a specification of each of the systems described in the figure and what each boundary means. Figure taken from [221].

A comprehensive predictive framework for ecosystems under global change

The main big challenge for ecological research that lies ahead is to understand and predict how global change is affecting and will likely affect complex ecosystems. We are now at the dawn of an era in which we need a deeper understanding of how complex natural communities are organised and how they work if we are to make accurate predictions about their stability and persistence in the face of different components of global change, and the synergistic effects these might produce when acting in tandem [215]. We need to understand not only how and why species are going extinct, but, perhaps equally importantly, what is happening to the interactions among the remaining ones.

In this thesis I try to tackle this challenge by first, pursuing an understanding of how perturbations such as climatic warming, species loss, biological invasions, and habitat loss and fragmentation, are likely to affect community structure and organisation; and second, by looking at how these changes in turn affect several components of community stability. As we have seen, the history of ecological theory has brought us to a point in which a good understanding of the factors influencing community dynamics and organisation has been achieved. We now know that the structure of the interactions between species in ecosystems and their strength are fundamental factors determining community persistence and stability. It is also clear that species traits are good potential candidates for explaining ecological interactions. An understanding of how different aspects of global change affect interactions and species traits must be thus essential ingredients of our research if we want to have any chance at predicting the effects

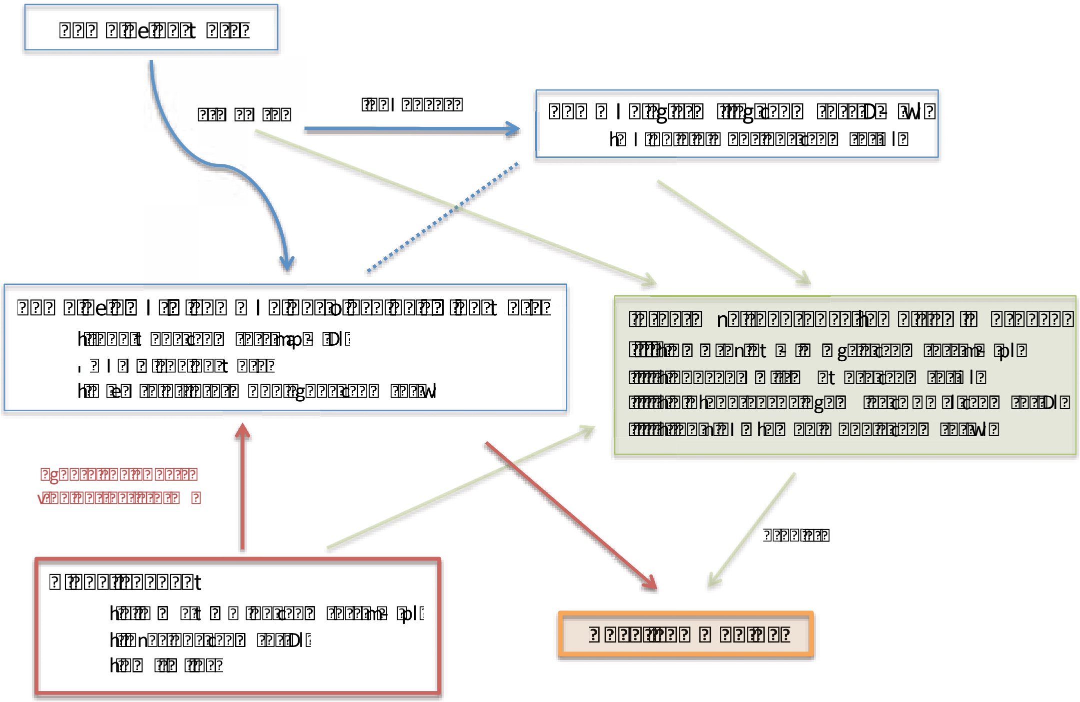


Figure 7: A predictive general framework for complex ecosystems responses to global change. Schematic representation of the research areas explored in this doctoral dissertation and the methodologies employed. Blue: Factors structuring and defining complex natural communities and their internal processes. Red: Global change on communities and its synergistic effects create novel communities. Green: All factors considered in the theoretical framework developed as part of this thesis. Open squares define the challenges tackled in the thesis. Filled squares describe the approach (green) and the phenomena to be predicted using this approximation (orange).

of a planetary shift on ecosystems. **The overall objective of this thesis is thus to develop a predictive general framework for predicting the effects of several components of global change on the organisation and dynamics of complex ecological networks, where interactions and species traits are fundamental** (figure 7). In box 1, a more detailed summary of the questions, approaches and main findings of this thesis can be found. I do not pretend this to be a finalised theory, but my hope is that after reading through this dissertation, the reader might be in a comfortable position to readily apply concepts, ideas and approximations into a pressing need: what is the extent of human impacts on natural communities and what are the best strategies to adopt in order to prevent a catastrophic phase transition in ecosystems worldwide.

Box 1: Summary of questions, approaches and main findings of this thesis

Question(s)	Approach	Results
What are the impacts of climate change on biotic interactions and food webs? (*Chapter 1 & 2*)	Literature review across ecosystems and interaction types, traits and patterns. Plus an in-depth study of altitudinal range expansions in empirical food webs.	Species range shifts are causing novel communities to arise. These are characterized by consistent novel patterns where body size distributions within the food webs are getting shifted towards smaller values, specialised interactions are getting lost -leading to a greater generality of consumer species-, and interaction strengths are getting stronger in general.
What is the relationship between different dimensions of ecological stability? (*Chapter 3*) Do these relationships change in the face of major disturbances? (*Chapter 3*)	New theoretical framework for the analysis of the correlations between different stability measures. Test with empirical food webs where species were removed following different sequences.	Different dimensions of ecological stability are correlated in non-trivial ways when they are measured on undisturbed communities. Biodiversity loss leads to a decoupling of the correlations previously observed between stability measures. This leads to highly unpredictable dynamics of ecological communities after disturbances.
What are the effects of biological invasions on complex food webs? (*Chapter 4*) Which food web characteristics and species traits most likely affect invasion success in multispecies communities? (*Chapter 4*)	Development of a theoretical bio-energetic food web model where in silico invasions are simulated.	Food web structure is a strong determinant of invasion success. Less connected, more modular, and more heterogeneous communities in terms of diet breadth are more robust to biological invasions. Invasions make communities more connected and less modular in general, rendering them even more fragile to invasions. Species traits of the invasive species, such as body size and the ability to capture prey, are strong determinants of invasion success.
Is the stability of communities affected by the balance of mutualistic and antagonistic interactions considered? (*Chapter 5*)	New individual-based spatially-explicit model with realistic food web structures.	Mutualistic interactions increase dynamic stability and spatial stability, by keeping spatial aggregation more constant. Distributions of interaction strengths across the entire ecological network are shifted towards lower values as mutualism increases.

How have I approached these issues: summary of chapters

This thesis is organised in 5 main chapters -plus the present introduction and some conclusions and final remarks-, each of which tackles a different aspect of global change and community organisation, employing an array of different methodologies and building progressively towards a comprehensive view of the subject. I employ an integrative theoretical-empirical approximation to deal with various facets of climate change and its effects on ecological communities (figure 7, box 1).

Chapter 1

In *Chapter 1* we look at the effects of climatic warming on the distribution of species across large spatial extents, and on how this is leading to novel communities with different interaction patterns and different distributions of species traits. Previous work demonstrated climatic warming is disrupting the distribution of species at the global scale. Species have shifted or expanded their ranges towards formerly cooler areas. They are tracking climates given that their previous distributions now include areas that are becoming too hot for them to survive, while at the same time new places with suitable habitats are becoming increasingly available due to these increases in temperature [193, 48]. This same phenomenon is also trapping species in places where they can no longer track climate (e.g. because habitats are increasingly fragmented) and are hence doomed to extinction if they do not cope with changing climate. We extend these observations to food webs of multiple interacting species and show how the distributions of trophic interactions and species traits -such as body size- are shifting due to the arrival or loss of species. By performing an extensive literature review, we offer a picture on how novel communities are being re-structured by climate change, identifying changes in their composition and pinpointing how they affect the structure of the interactions in these communities.

We identify general patterns and major unknowns on the structure and dynamics of novel communities that result from climate change. First we focus on closed communities, where we assume that populations cannot track changing climates across space by dispersal. Species in these communities can then either ‘stay and adapt’ or ‘stay and become extinct’. **We find that climate change in closed ecosystems is (i) shifting body size distributions within these communities towards lower values; (ii) affecting primarily specialised interactions; and (iii) making consumer-resource interactions stronger in general**. We then move to open communities and look at how changes prompted by climate change affect both source -i.e. where do species come from- and sink -i.e. where do species arrive- communities. One of the major unknowns identified is the fact that we still do not know whether large-bodied or more generalist species are able to shift their ranges faster and further due to mixed evidence for different taxa. We observe that the movement of large-bodied species is decreasing body size distributions in source communities, while shifting it towards larger values in sink communities. Also, climate change is prompting the loss of specialised interactions in sink and source communities; and a decrease and an increase of interactions strengths in source and sink communities respectively. **In general, novel source communities are losing generalist consumers, while novel sink communities are incorporating new interactions for generalist consumers and are facilitating the existence of new species due to enemy release**.

Chapter 2

In *Chapter 2*, we look into the effects of climate warming over the structure of the food web of a mountain ecosystem in the Pyrenees (northern Spain). Over the last 40 years, this area has experienced a mean annual temperature increase of about $1\,^{\circ}C$. These changes affect different species in different ways, with interacting species shifting their ranges at different speeds, producing in this way spatial mismatches between species that were previously part of the same community. **A major challenge is to predict which species will more likely expand their ranges, whether range expanders have particular traits and the consequences of differential range expansion on the structure and dynamics of the food web within which these species are embedded**. To tackle this issue, we use empirical data from publicly available databases to construct networks of trophic interactions between species living at three different altitudinal ranges over a period of 20 years of warming. We then relate temperature data for these three ranges over that same period of time to changes in species composition, and the corresponding changes in food web structure, at each of those ranges. We found that temperature increase has facilitated the range expansion of numerous species across the altitudinal range, in line with previous observations in other mountain ecosystems (e.g. [171]). This range expansion has caused communities at higher altitudinal ranges to become more speciose and more heterogeneous in terms of diet breadth and number of predators per species. It has also prompted the loss of generalist species at low and intermediate elevations, and a decrease in prey vulnerability (i.e. number of attacking predators) across all elevations. Communities have gained large-bodied species in general, which has prompted a shift in body sizes distributions towards larger values. This is mainly due to large prey species migrating, which tend to be bigger than native prey. This in turn has altered predator:prey mass ratios in non-intuitive ways, by shifting their distributions towards smaller values in low and intermediate altitudinal ranges and towards larger ones at high elevations. These results agree with our findings from *Chapter 1* in several aspects.

Chapter 3

Chapter 3 focuses on the relationships between different dimensions of ecological stability and how these relationships are upset when perturbations are applied to the system. We integrate in a common conceptual framework several measures of stability as those proposed by Pimm in 1984 [202], including some additional ones. Specifically, we looked at: temporal and spatial variability, compositional turnover, robustness (measured as the number of extinctions), number of invasions, and resistance. This conceptual framework is then employed to understand how stability measures are correlated in natural systems. Using data from experimental manipulations on intertidal enclosures [184] we analyse how correlations between different stability measures are decoupled under different perturbation regimes. We find that, **after a perturbation (biodiversity loss in this case) the different measures of stability, which until then (before the perturbation) were correlated, loose these correlations. This makes the system more unpredictable, since it is no longer possible to predict what will happen to other components of stability by only looking at a single one**. We end this chapter by offering a framework on the dimensionality of ecological stability that can be employed by ecologists when looking at the effects of perturbations on ecological systems to assess the extent of these effects by considering the changes in correlation between different stability measures. The idea of multi-stability in ecological systems is akin to the concept of multi-functioning recently developed in biodiversity-ecosystem functioning research [96]. These results suggest that multiple aspects of ecosystem functioning might be correlated, and that biodiversity loss might affect these systems in such a way that their multiple functions would no longer be predictable only by looking at a single one.

Chapter 4

In *Chapter 4*, we move towards more theoretical grounds while at the same time shifting our attention towards another key component of global change: biological invasions. Biological invasions are one of the main threats to biodiversity and ecosystem organisation worldwide. It is a main component of global change and is changing communities composition at an accelerated pace. It is the kind of big perturbations that when applied to natural communities has the potential of pushing it to a phase transition of a different kind of those seen traditionally in this kind of self-organised system. For this reason, it is important to develop dynamical approximations that are capable of giving us a clear idea of the many consequences of this type of perturbation on complex ecosystems.

We tackle this issue by employing a theoretical framework that mixes a model for the construction of realistically structured food webs, similar in spirit to that proposed by Cohen in the 90s [51], with an expanded version of the bio-energetic model originally developed by Yodzis and Innes [283]. For the generation of the networks of trophic interactions between species in our communities we employ the niche model [272]; a model for food web generation grounded on the idea that species can be ordered in a continuous one-dimensional ‘niche’ and interactions amongst these species can be determined by the connectivity of the network following a simple heuristic for link assignment. For simulating population dynamics we used an allometric version of the bio-energetic model, which incorporates an allometric (based on body size) derivation of certain key parameters according to the metabolic theory of ecology [41]. We perform a comprehensive set of *in-silico* invasion experiments over complex communities simulated in this way to obtain a clear picture on how network complexity and species traits mediate the effects of biological invasions on food webs. **We find that several properties of the food web, some of which are related to the stability of the community, such as connectance (i.e. the fraction of realised amongst the possible links in the network), number of food chains, or modularity, are consistently good predictors of community robustness against invasions**. Connectance, for example, was shown to have a negative effect on resistance to invasions: less connected communities were more robust against invasions. Interestingly, this contradicts some of the ideas traditionally held in community ecology (see above) on the increased resistance to perturbations on more complex communities. In particular, Pimm [203] found that more connected communities were more resistant to invasions. The key difference between this work and Pimms is the size of the community. These results taken together suggest that complexity confers robustness to ecological communities until a species-richness limit is reached, after which a decrease in complexity is required to achieve resistance.

One of the key findings of this chapter is that **those same properties of food web structure that are good predictors of invasion success change consistently due to invasion. And they change in such a way as to make the resulting communities even more fragile against invasions, according to the effects of these properties on invasion success**. Biological invasions are making complex ecological communities more fragile and less stable due to specific changes in food web structure. We also find that several traits of the invasive species, such as body size or the ability to capture prey, are important determinants of invasion success. It is also worth noting that different components of stability in these communities are affected in different ways by network connectivity after invasion, suggesting that different dimensions of community stability react differently to ecological perturbations.

Chapter 5

Finally, in *Chapter 5*, we investigate the effects of two particular ecological aspects over community stability: space and diversity of interaction types. The incorporation of space allows us for looking at the stability of communities from a different perspective: spatial stability, and to its relationship to other kinds of stability and to the structure of the ecological network. Mixing different interactions types in the same ecological network, on the other hand, allows us to look at the effects of the balance of positive and negative interactions on community stability. In order to include space into our experiments we once again change gears in our approximation. Traditionally, the behaviour of dynamical systems is analysed using sets of ordinary differential equations to simulate the rate of change of some variables of interest through time. This is the kind of approximation we employ in *Chapter 4*. However, another way of looking at dynamical behaviour of systems of interacting entities however, is by **focusing on interactions occurring at a local scale, following local rules**, rather than being specified at the system level via some mathematical equation.

This way of performing computation was firstly envisioned by John von Neumann in 1952 [266]. At that time von Neumman was interested in the origin of life and he wanted to come up with an explanation for the process of self-replication, particularly looking at how self-replication could occur in machines. He found that only by following very simple local rules his cellular automata (CA), as he called them, were able to produce copies of themselves. What he did not suspect was that his idea would turn into one of the greatest scientific thought-shifting paradigms of modern science. One that would make scientists start thinking in terms of local rules and interactions and how these can, first of all perform operations in the same fashion as an universal computer and, second, produce interesting emergent patterns [276]. The emergence of intelligent behaviour in systems of interacting autonomous entities following certain rules has long been a research topic in computer science and artificial intelligence. Yet, its application to the study of phenomena in other areas of the sciences had been limited until recently. In ecology in particular, this approximation to the study of ecological systems is known as individual-based modelling [88], where species populations are modelled as aggregations of individuals that follow certain rules of interactions.

In this chapter we thus develop a **new spatially-explicit individual based model** in which individuals belonging to different species in a complex ecological network interact according to certain rules given by their possible interactions in the web and some bio-energetic constraints. These individuals ‘live’ in a 2D grid in which the state of each cell is basically the identity of the species the individual occupying that cell belongs to. The model thus behaves as a very complicated CA in which only these interaction rules between individuals acting at the local scale are responsible for the system-level emergent behaviour ultimately displayed by the system. As in the previous chapter (*Chapter 4*) we generate realistic networks of interactions between species in our artificial communities using the niche model. Following a methodical heuristic we then choose some of the interactions in the network and consider them as mutualistic, in order to construct a comprehensive ecological network with a mixture of interaction types (trophic and mutualistic interactions). We perform a series of simulation experiments using this model in which different proportions of mutualistic interactions are present in each of the communities modelled. This allows us to assess the effect of mutualistic interactions on community assembly and of different mixings of interaction types over several components of stability. We find that, as previously observed by other authors [172], the proportion of mutualistic interactions within the broader ecological networks has profound consequences for community stability.

Communities simulated in this way display rank-abundance distributions close to those traditionally found in natural communities (lognormal distributions) and also, the cumulative degree distributions of the interaction networks follows patterns observed in nature (exponential distributions). A model constructed in this way provides thus with an ecologically realistic basis for performing the experiments described above. Communities with larger fractions of mutualistic interactions are more stable in general. We find a **negative relationship between the fraction of mutualistic interactions and May's measure of complexity** -$< i > (SC)^{1/2}$, where S is species richness, C is network connectivity and $< i >$ is the mean of interaction strengths-, which given that our communities have the same number of species and connectance, suggests that the **strength of interactions decreases as mutualism increases** in these model communities. Indeed, we find a shift of the distribution of interaction strengths towards lower values as the fraction of mutualistic interactions in the network increases.

Space is of fundamental importance for ecological communities given that many processes occurring at the individual interactions' level are driven by spatial location: predation, mating, social interactions, among others. In addition to its recognised stabilising potential for ecological communities [102, 237], space (considered explicitly) facilitates the incorporation of other measures of stability into our analysis. We find that even when the degree of mutualism in our communities does not have a noticeable effect on the spatial distribution and density of populations in the model communities, spatial aggregation is positively affected by it. **This suggests that processes that can be facilitated by the aggregation of individuals such as reproduction could be favoured by the presence of mutualistic interactions in the community. Spatial stability, measured as increased spatial aggregation in populations is thus positively affected by mutualisms in these model communities**.

These results provide interesting clues about the 'devious strategies' used by nature to confer complex ecosystems with stability and persistence. Intriguingly, we again find that, similar to our findings in the previous chapter, different dimensions of community stability are affected differently by increases in the proportion of mutualistic interactions.

Chapter 1

Novel communities from climate change

Miguel Lurgi, Bernat C. López, José M. Montoya

Philosophical Transactions of the Royal Society B: Biological Sciences (2012), **367**:
2913–2922

Abstract

Climate change is generating novel communities composed of new combinations of species. These result from different degrees of species adaptations to changing biotic and abiotic conditions, and from differential range shifts of species. To determine whether the responses of organisms are determined by particular species traits and how species interactions and community dynamics are likely to be disrupted is a challenge. Here, we focus on two key traits: body size and ecological specialization. We present theoretical expectations and empirical evidence on how climate change affects these traits within communities. We then explore how these traits predispose species to shift or expand their distribution ranges, and associated changes on community size structure, food web organization and dynamics. We identify three major broad changes: (i) Shift in the distribution of body sizes towards smaller sizes, (ii) dominance of generalized interactions and the loss of specialized interactions, and (iii) changes in the balance of strong and weak interaction strengths in the short term. We finally identify two major uncertainties: (i) whether large-bodied species tend to preferentially shift their ranges more than small-bodied ones, and (ii) how interaction strengths will change in the long term and in the case of newly interacting species.

1.1 Introduction

Climate change affects different levels of biological organization. Early studies focused on population and species-level effects, and showed species range pole- and up-ward expansions following temperatures as climate warms, together with a number of phenological changes [193, 268, 48]. There is still a lack of strong and coherent theoretical and empirical foundation to incorporate species interactions and traits into climate change research [60]. This incorporation is crucial to develop better understanding, ecological forecasting and conservation planning of natural ecosystems.

Community- and ecosystem-level effects of climate change have received considerable attention over the last years, with a focus on how climate change affects species interactions and ecosystem processes [268, 163, 280]. At this level of biological organization, a fundamental question arises: Are there general patterns in the way species respond to climate change within and across ecosystems, or are responses merely idiosyncratic -i.e. each species responds differently? To answer this question, the challenge is to identify organism traits that may determine their sensitivity to climate change, and the consequences of their responses for species interactions.

If coexisting species have different sensitivities and differential responses to climate change, there will certainly be an emergence of new ecosystems with novel species combinations and/or changes in the distribution and strength of their interactions. This will probably alter their abundances, distributions and extinction probabilities [60]. However, our present understanding of the effects of climate change on species interactions in ecosystems is mired in idiosyncratic case studies and focused mainly on very small species interaction modules (e.g. reviewed in [163, 86]).

Here, we ask whether it is possible to identify traits responsible for the differential sensitivities of species to climate change, and, on the basis of this, what novel communities from climate change would look like. We focus on two particular traits: species body size and diet specialization (i.e. diet breadth), presenting theoretical expectations and empirical evidence for the existence of trait-mediated sensitivities.

Body size is a commonly available surrogate of relevant life-history characteristics of species, namely dispersal ability, reproduction timing and frequency, population abundance or metabolism [278]. It is also a trait known to affect a number of biological processes, from the individual to the ecosystem level, including metabolism, fecundity, population growth rate, population density, trophic flows or ecosystem respiration [278, 40]. Within trophic interaction networks, a number of studies have reported that body size determines food web structure and dynamics (see [37] for a review). For example, large predators tend to interact with more diverse prey items than smaller ones, and predator-prey size ratios determine biomass flux and interaction strength, ultimately regulating food web dynamics.

Declining body size is suggested as the third ecological universal response to warming, following poleward and altitudinal range shifts and species phenological changes [56, 84, 233]. Similarly, changes in community size structure are likely to exert profound changes in the topology and dynamics of ecological networks [37]. Here, we will explore these changes and their likely consequences on novel communities in the face of climate change.

Diet breadth is a fundamental dimension of a species niche, and the balance of generalist and specialist species within communities determines the structure of species interaction networks and ecosystem functioning [162, 219]. Diet breadth is systematically related to body size in food webs across ecosystem types [65], with larger predators feeding on more prey items than smaller ones. It is also likely that diet breadth is the key for predicting how species cope with climate change. For example, specialist enemies or mutualists with obligate interactions can be limited by other species when they shift their distribution range as climate changes, while generalists should be less constrained [68]. Along this line, the extinction risk of species, in the absence of warming, increases with the level of specialization in terms of the number of prey and the range in body sizes of the prey [23].

In this chapter, we aim at identifying general patterns and major unknowns on the structure and dynamics of novel communities that result from climate change. The chapter is structured in three sections. The first section deals with climate warming impacts within closed and local communities, where we assume that populations cannot track changing climates across space by dispersal. Within closed communities, species can stay and adapt or stay and become extinct. In particular, we ask (i) whether climate change is reducing body size within populations and communities, (ii) whether there is a preferential loss of specialized interactions, and (iii) whether climate change affects consumer-resource interaction strengths.

The second section incorporates species movement as climate changes, considering open communities with species migration. In this section, we investigate which species are more likely to move and what are the consequences of differential species range shifts on the structure and dynamics of source and sink communities. In particular, we explore (i) whether larger species shift their ranges faster and further, (ii) whether trophic generalists are more likely to track changing climates, and (iii) to what extent interactions are lost or gained as species migrate. The last section tries to summarize and connect the general patterns observed as well as the major unknowns identified in novel communities resulting from climate change. The implications of these patterns and unknowns for food web structure and dynamics and for community size structure are also discussed.

1.2 Closed communities

Closed communities with negligible immigration rarely exist in nature, with some oceanic islands or isolated mountain ranges as exceptional examples. However, climate change is acting on already highly degraded and fragmented landscapes, where species movements are constrained. In this section, we explore the effects of climate change on local communities where species are not tracking climate in space, in order to establish the baseline of local climate change effects making the simplifying assumption that species are not moving.

1.2.1 Climate change and body size shifts within populations and communities

There are (at least) four rules concerning relationships between body size and temperature that are relevant in this context. The first three are summarized in [56], and are based on biogeographic and ecothermal gradients: first, Bergmanns rule (which states that warm regions tend to be inhabited by small-sized species); second, James rule (saying that populations with smaller body size within a species are more likely to be found in warmer environments); third, the temperature-size rule (stating that the average size of individual ectotherms is inversely related to temperature [8]). The fourth one is the allometric size-scaling rule, which states that warming should lead to a decrease in the mean body mass and/or a decrease of population abundance at equilibrium [40]. Collectively, these rules predict that warming will reduce species body size and shift community size-structure towards smaller size-classes.

Starting at the population level, two recent reviews have shown heterogeneity in both the magnitude and the direction of size responses to warming [84, 233]. The degree to which organism size is affected by temperature varies across taxa, but some general patterns can be recognized.

Both terrestrial and aquatic ectotherms have shown decreases in their body size. Numerous experiments have exposed organisms to increasing temperatures, and have shown decreases in species body size, including marine invertebrates, fish, beetles and salamanders, compared with controls ([233] and references therein). Both the rate and degree of shrinkage varies widely between taxa: from 1 - 3% in beetles to 14% in salamanders for each degree Celsius of warming. Evidence for mammals and birds also supports shrinking body sizes as the climate warms [233], although some works show equivocal responses or no change at all [84, 226]. Only in some exceptional cases, the opposite trend is observed, with increasing body sizes for certain fish, lizards, birds and mammals. Along this line, studies such as those by Yom-Tov and collaborators [285, 284] have shown an increase in body size in medium and small mammals (otters and shrews, respectively), with increasing temperatures during the last decades. The hypothesized mechanism behind this was an increase in productivity over the whole ecosystem owing to increasing temperatures, which in turn facilitated an increase in species body size. Most of these exceptions are from high latitudes [233, 277], and it is expected that species inhabiting areas where increasing temperature and precipitation will lead to increased net primary productivity are likely to exhibit less clear shrinkage patterns.

Population and species body size changes would affect the distribution of body sizes at the community level. As expected from the previous rules and evidence at the species level, warming is likely to favour small ectotherms to the detriment of large ones. This has been observed across different trophic levels. A recent meta-analysis revealed that mean body size of high trophic levels, fish in large French rivers in particular, has decreased significantly during the last 2-3 decades under gradual warming.

In lower trophic levels, increasing temperatures decreased bacteria and phytoplankton cell size in temperature-controlled mesocosms [56]. Similarly, diatom cell size has decreased with increasing temperatures through the fossil record, suggesting that impending warming will shift phytoplankton communities towards smaller cells, where diatoms would be at a competitive disadvantage [78]. In another study, picophytoplankton (which comprise cyanobacteria and eukaryotic algae smaller than 2 mm) increased with temperature along a natural temperature gradient in the ocean, regardless of differences in trophic status or in inorganic nutrient loading [169]. Finally, studies in one of the areas experiencing the most extreme climatic warming on Earth, the Western Antarctic Peninsula, have shown that over the last 30 years there has been an increasing fraction of the largest components of phytoplankton, including diatoms and other large cells, in the southern (colder) region than in the northern (warmer) one [161].

Although climate change can affect different trophic levels within the food web, experiments considering multi-trophic communities have shown that warming does not affect the size-structure of different trophic levels equally. In a freshwater mesocosm study simulating expected warming for the end of the present century, mean phytoplankton body mass decreased by an order of magnitude between control and $4\,^{\circ}\mathrm{C}$-warmed treatments, while mean zooplankton body mass remained constant. Compositional changes were observed, with warmed communities characterized by small phytoplankton species and by the absence of large species that were commonly found in controls. This compositional turnover was not observed for the zooplankton.

This result seems to contradict previous findings of higher trophic levels more sensitive to climate change than lower trophic levels [200], with larger extinction probabilities of higher trophic levels within bacteria-protist microcosms [200]. This apparent contradiction might be due to the combination of resource availability under warm conditions and close-to-lethal and lethal temperatures of different organisms. Higher metabolic demands of consumers high in the food web triggered by warming need to be compensated by higher availability of resources down the food web; otherwise, consumers will starve and eventually disappear. Yvon-Durocher *et al.* [286] showed a decrease in phytoplankton biomass, but it was compensated by an increase in phytoplankton turnover rate (as expected from the dominance of small organisms), and thus it was able to fuel higher zooplankton requirements with no concomitant effects higher up in the food web.

1.2.2 Lost and new interactions in closed communities

Phenological mismatches and dietary shifts

Differential responses of interacting species to climate change are affecting temporal/phenological coupling and decoupling, and are changing also consumer diets. This will eventually lead to the reorganization of consumer-resource interactions in ecological networks, with some interactions lost and new links emerging. Although idiosyncratic responses are sometimes claimed [280], it is important to search for general patterns. We discuss here how phenological mismatches and dietary shifts are related to species traits such as trophic position and diet breadth.

Habitat generalists with broader ecological niches have been shown to cope better with environmental change than specialist species with narrower ecological niches. In the past 10 years, numerous studies have reported that, in many ecosystems, generalist species are replacing specialist species, as predicted by niche theory, and causing biotic homogenization [50]. A reasonable assumption is that generalism in habitat use reflects broader diet breadth, and hence diet specialists should be more sensitive to climate change within closed communities than diet generalists. Phenological mismatches have been found in plant-pollinator mutualisms [157], plant-insect interactions [262] and multi-trophic interactions [32]. Climate-driven phenological changes on higher trophic levels (i.e. secondary consumers) are slower than at lower trophic levels (with the exception of woody plant species), making the former especially vulnerable to phenological decoupling, as revealed in a recent review of terrestrial and aquatic ecosystems in the UK [248]. This is even more apparent when complex food chains consisting of several (more than two) trophic levels are considered.

Phenological changes across trophic levels in a European deciduous forest over 25 years showed that the phenological phases of tree budburst advanced only slightly, while the next two trophic levels, the herbivores (represented by caterpillar biomass peaks) and insectivorous birds (represented by their hatching day), have advanced [32].

Diet specialists can be more severely affected by climate change than generalists. This has been documented for butterfly species with narrower larval diet breadth (i.e. number of food plant species), which have experienced relatively greater advances in their phenology than generalist butterflies [62]. Interestingly, other components of global change, namely the degree of intensification of human land use and aridity, affect generalist butterflies more severely than does climate change, while specialized butterflies showed serious richness and population declines with increasing temperatures [241].

Climate change is also producing dietary shifts on consumers. For generalist consumers, dietary shifts can simply reflect changes in the relative abundance of their prey as climate warms. These changes are characterized by Rall *et al.* [216] as a dominance of smaller prey items in consumers diet. This has been shown for several apex predators in different habitats experiencing changes in ambient temperature. Trout in Arctic freshwater food webs showed marked changes in the invertebrate prey they fed upon along a natural temperature gradient [277]. Similarly, California sea lions shifted their diet composition from one dominated by market squid (Loligo opalescens), anchovy and rockfish to a diet predominantly composed of smaller sardines, rockfish and hake species [270]. Finally, 40 years of increasing temperatures affecting five apex predators in the Bering Sea, including fur seals, two species of kittiwakes and two species of murres [236], changed their diet to a predominance of pollock species of small size [236].

1.2.3 Climate change and interaction strength

Climate change may also disrupt the strength of interactions among species, ultimately affecting community dynamics and functioning. Feeding rates depend on body mass and temperature (see [216] for a recent compilation of different functional responses). There are theoretical frameworks to investigate the effects of increasing temperatures on predator-prey interactions [216, 258]. Vasseur & McCann [258] modelled consumer-resource dynamics, where metabolism and body size were dependent upon temperature, ultimately increasing consumer ingestion rate which shifted the system from a stable into an unstable (cycling) state. However, these authors assumed that the activation energy of consumption is higher than that of metabolism, which is not supported by recent meta-analyses [216, 253]. In some cases, warming can stabilize population dynamics [24]. As a general theoretical expectation, increasing temperatures are likely to change the distribution of interaction strengths, with some interactions likely to become stronger.

Most empirical studies support this theoretical expectation, although evidence is not unequivocal. Top-down effects seem to get stronger as climate warms both in aquatic and terrestrial systems. In a seminal experiment, a marked increase in ingestion rates for the keystone predator seastar *Pisaster* of the dominant prey *Mytilus* was observed with higher water surface temperatures [227]. Similarly, warming increased the per capita interaction strength of the grazing amphipod *Ampithoe longimana* on the common macroalga *Sargassum lipendula* [179].

More generally, O'Connor and collaborators [180] showed that despite increases in primary productivity, warming strengthened consumer control of primary producers in a marine food web. This was due to shifts in food web structure towards greater heterotroph biomass relative to autotroph biomass, consistent with predictions based on the differential temperature scaling of respiration and photosynthesis metabolism [286, 137, 287].

Other authors found a somewhat similar effect of temperature on a predator-prey relationship between an insect and its larval anuran prey [5]. In this case, the proposed mechanisms behind the change in the interaction strength were different. An increase in temperature produced a general increase in the body size of the prey and this, in turn, rendered the gape-limited predator less able to capture prey. Tadpoles of a given size experienced a higher probability of capture, which had the potential of increasing the strength of this interaction. The overall effect of rising temperatures was a weakening of this predator-prey relationship, but there were direct as well as indirect effects involved in its change.

Warming is likely to affect both top-down and bottom-up control, but to a different extent. In greenhouse experiments using the aquatic community found in pitcher plants (*Sarracenia purpurea*), for example, warming increased mosquito predation on protozoa populations [100]. In contrast, bottom-up effects on protozoa were unaffected by temperature. Similarly, in terrestrial systems, Barton and co-workers considered direct and indirect effects in an old-field food web, showing that increasing temperatures did not change primary production, but the strength of top-down indirect effects on grasses and forbs increased by 30 - 40% per 1 °C [11].

Whether bottom-up effects are generally unaffected by warming while top-down effects are strengthened requires further theoretical and empirical exploration (see [234]). Yet, if temperature influences the relative importance of top-down versus bottom-up effects, this would have major consequences for community dynamics and species persistence.

Changes in interaction strength are also a matter of time. In a series of theoretical and experimental s, Rall and co-workers [217, 267] showed that increasing temperatures tend to increase predator ingestion rate and per capita interaction strength in the short-term, while in the long-term temperature is likely to decrease interaction strength. They provide an elegant explanation by synthesizing metabolic and functional-response theory corroborated with experiments with terrestrial arthropods (beetles and spiders). What happens is that warming imposes energetic restrictions on predators in the long term by decreasing their energetic efficiencies (the ratio of feeding to metabolism), ultimately reducing interaction strength. However, this should be further explored, because in the long term other processes may compensate for increasing metabolism, such as increases in prey abundance or turnover rate [287].

The effects of temperature on the strength of interactions may depend not only on the amount of the increase in temperature, but also on the time of exposure to these regimes. Pincebourde *et al.* [209] found that chronic exposures to high temperatures decreased the predatory pressure of *Pisaster* over *Mytilus*, whereas an acute exposure had an inverse effect, increasing the strength of this trophic interaction. This is particularly relevant to the study of ecosystems with highly variable intra-annual temperature regimes, where climatic warming may have opposite effects on interaction strengths in different times of the year.

1.3 Open communities

The overall picture in open communities is more complex, however, because some species will spatially track changing climates, while others will not, and thus dispersal differences among species will act on top of changes observed in closed communities. In this section, we consider whether species shifting (mostly expanding) their ranges are characterized by specific traits. We also consider the nature of new and lost species interactions resulting from these differential range shifts.

1.3.1 A few generalities on species range shifts tracking climate change

Species range shifts are perhaps the best documented biological response to climatic warming to date, but there is little consensus regarding the extent to which different organisms will be able to establish populations in newly suitable habitats. This is particularly important given the rapid rate of climate change. Mounting evidence shows that species ranges follow changing climates, with most observations coming from latitudinal or elevation shifts from temperate species [193, 268].

Over the last *lustrum*, some studies have demonstrated species differential range shifts leading to spatial mismatches as a consequence of warming. This has led to similar consequences as those observed in closed communities, i.e. the formation of non-analogue communities, with new combinations of existing species and a re-mixing of species interactions [163].

Which traits predispose species to better track climate change? Intuitively, greater dispersal ability could increase the rate of spread, and better dispersers should be capable of tracking climate change more effectively and rapidly. But dispersal distance is difficult to quantify because rare long-distance dispersal events can have a disproportionate effect on the overall rate of spread [49].

Other life-history characteristics such as early reproduction, frequent reproduction and high fecundity should also increase colonization opportunity [7]. Details on most of these traits are lacking for most species, and to be useful for forecasting variation in responses to climate change, such knowledge should be available across many taxa and geographical regions. An alternative is to rely on more commonly available surrogates of relevant life-history characteristics. Here, we focus on two of them: body size and ecological specialization.

1.3.2 Do larger species migrate faster and further?

Body size shows positive correlations with some traits affecting the potential for shifting ranges under warming, including dispersal ability, home range size, trophic level, fecundity or competitive ability [40]. The general expectation should therefore be that larger species are more likely to migrate tracking climate changes, and they will be able to establish in new environments.

The natural experiment provided by the Late Pleistocene glaciation event is a good starting point to assess evidence. Roy and collaborators [115] analysed the range shifts of Californian marine bivalves from this period, and found that large-bodied species were more likely to shift their distribution in response to climate change. A similar pattern was observed for mammals over the same time period, with a positive correlation between range centroid distance shift and species body size [145]. Interestingly, these authors found that small-bodied species show a great deal of variation in the distance that they shift their range, with some having range shifts as large as some of the largest species [145] By contrast, large-bodied species have much less variation in the distance they shifted their ranges.

Responses to recent climate change, however, are less unequivocal. Noticeably, only a few studies have explored differential range shifts related to species body size. Large butterflies, measured as female wing length, have shifted ranges more than small butterflies in Finland between two time periods (1992-1996 and 2000-2004) [212]. However, a recent meta-analysis [7] has shown that at expanding range edges, body size has very low explanatory power for range expansion for datasets of diverse taxa, including North American Passeriformes, British Odonata and western North American small mammals (see also [143]).

Some studies actually show the opposite pattern. Pole-ward range margin shift of 116 southern Finnish bird species was larger for small-bodied species [36]. Similarly, North Sea fish species with shifting distributions tended to have smaller body sizes and faster life cycles, reflected in faster maturation and smaller sizes at maturity than non-shifting species [198].

No clear trend is therefore evident from the available data. A possible explanation is that, while some traits that are positively correlated with body size predispose large species to track climate changes in space, other traits benefit the establishment of small organisms. For example, traits that are likely to increase colonization opportunity, such as frequent reproduction and high propagule pressure, are usually negatively correlated with body size. As a conclusion, it will be the balance between beneficial and detrimental traits correlated with body size that determines whether large species will be able to move further and faster.

1.3.3 Generalism, specialism and range shifts

Species with specialized niches and highly co-evolved interactions that have resulted in strong specializations might encounter great difficulty establishing populations in new habitats as they expand their ranges. On the contrary, ecological generalists with broader diet breadths will more easily find suitable resources and realized interactions in their new location. In addition, polyphagy may enhance the ability of species to track climate change. The flexibility of polyphagous generalist species with the incorporation of novel hosts may result in species having greatly enhanced abilities to track climate changes, leading to unexpectedly rapid range expansion.

A clear relationship exists between habitat generalists and diet generalists: species living in more habitat types will tend to have a broader resource range, as is the case for British butterflies [159]. Mounting evidence shows that habitat generalists shift ranges more easily than habitat specialists [18]. However, limited data exist directly on the dispersal abilities and degree of specialization for most species (but see [143] for an exception).

In a recent meta-analysis by Angert *et al.* [7], diet breadth was a good predictor of range expansion for North American Passeriformes, with generalists moving further than specialist species. However, diet breadth was a poor predictor for other taxa, e.g. western North American mammals. Similarly, the generalist butterfly *Polygonia c-album*, which is showing the greatest range expansion of any butterfly in Britain during on-going climate warming, has altered its host plant preference [33]. Current range expansion of this species is associated with the exploitation of more widespread host plants on which performance is improved. In addition, widely distributed host-plant generalist noctuid moths were more mobile than host-plant specialists with more restricted distributions [22]. In summary, diet breadth may or may not be a good predictor, depending on the taxa considered: good for birds, butterflies and moths, bad for small mammals. As a conclusion, diet breadth is a good candidate predictive trait for more mobile taxa (birds, some groups of flying insects) and a poor predictor for less mobile taxa such as small mammals [230].

1.3.4 Novel interactions and ecological release

We have seen before how climate change within closed communities can break existing species interactions and create new ones. The differential range shifts of species also remove and add interactions, both in the source (where species are coming from) and sink (where species arrive) communities (figure 1.1). It is hypothesized [86, 167] that climate change could create ecological release for species that track changing temperatures better than their enemies. Victims can leave their natural enemies behind during a range expansion [32, 167, 255].

Research conducted in soil communities support this hypothesis. A number of range-shifting plant species have less negative soil feedback in their expansion range than related native species [255]. For example, *Tragopogon dubius* is currently expanding from southern into northern West Europe. Along this expansion range, the plant has a better performance than closely related *T. pratensis*, which has a natural occurrence along the entire latitudinal gradient, owing to a combination of release from soil-borne enemies from its original range and accumulation of beneficial soil-borne organisms from the expanding range [255].

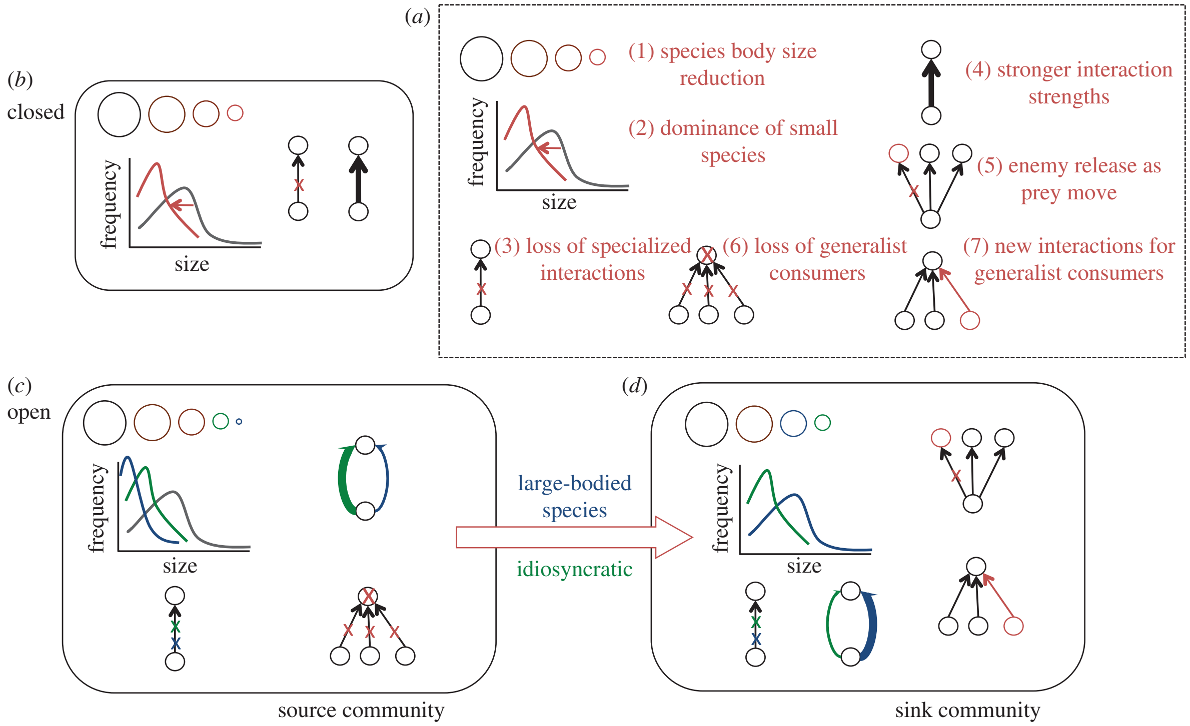


Figure 1.1: A summary of expected and unknown changes in size- and food web-structure in novel communities as a consequence of climate change. Cartoons in (a) correspond to the suite of changes addressed in this review. These include (1) reduction in species body size (population-level effect), (2) shifts in community size-distribution towards a dominance of small organisms, (3) loss of specialized reciprocal interactions, (4) increase in the strength of consumer-resource interactions, (5) enemy release as prey shift their ranges, (6) loss of consumers with broad diets as they preferably shift their ranges, and (7) appearance of novel interactions among migrating generalist consumers and native resources. Red colour indicates changes expected from climate change. (b) Corresponds to changes within closed communities as discussed in the main text. Lower panels correspond to open communities. For simplicity, it is illustrated with a source (c) and a sink (d) community, where, in addition to changes observed in closed communities, we consider changes due to migration of species from the source to the sink community, with no new species entering the source or leaving the sink community respectively. Two migration scenarios are considered to contemplate one of the major unknowns identified in our review: the preferential migration of large-bodied species (in blue) and the non-preferential, or idiosyncratic, migration of species -i.e. irrespective of their body size (in green). Changes in the source community are detailed in the main text.

However, one of the biggest unknowns of range-expanding species is whether and of what nature new interactions with natives will be. Although theoretical explorations are available [167, 121], direct empirical evidence is lacking. Lurgi *et al.* [143] is an exception, showing that most vertebrates migrating upwards in mountains as a consequence of climate change tend to interact with a more restricted suite of species than native vertebrates, modifying fundamental food web properties. Novel interactions can have a large influence on fitness because moving species lack co-evolutionary history with the new partner. This can cause local extinctions (e.g. increase in predation rates) but also might permit persistence otherwise impossible (e.g. a novel prey expanding into a predators range) [86].

1.4 Discussion and Conclusions

Evidence presented here shows that species within a community will not respond equally to climate change. Some may adapt better and some may track changing climates faster than others. These responses will not be merely idiosyncratic, and species traits such as diet specialism and, to a lesser extent, body size are good predictors of which and how species will adapt to changing conditions. Differential species responses will affect the structure and dynamics of species interaction networks both by breaking already established interactions and by the appearance of novel interactions, as we discuss in this section.

In summary, we have identified three major expected broad changes and two major unknowns of novel ecosystems from climate change, which are illustrated in figure 1.1. For simplicity, let us consider an open system composed of a source community (figure 1.1c) from which species migrate and a sink community (figure 1.1d) where those species that shift their ranges arrive. This, of course, is an extreme and simplified example, because some species may simply expand their ranges, and thus will not disappear entirely from the source community.

The first expected broad change is the shift in the distribution of body sizes towards smaller sizes. Locally (within closed communities, figure 1.1b), most available evidence reports shrinking body sizes and a larger dominance of smaller species with respect to larger ones. However, we identified a first major unknown that might compensate for or exacerbate this reduction: will large-bodied species tend to preferentially shift (or expand) their ranges more than small-bodied ones? If they will, the source community will be characterized by a size distribution even more extreme due to the combination of shrinking body sizes at the population level and the loss of large species from the community due to migration (figure 1.1c in blue). Sink communities will in turn compensate for shrinking body sizes within populations with the arrival of large species, resulting in small changes in community size distribution but important compositional changes. In particular, former large species in the food web will reduce their size and be replaced by those that have expanded their ranges. The alternative scenario, i.e. idiosyncratic migration not related to body size, will result in similar community size-structure of the source and sink communities (figure 1.1c in green).

The second pattern is that the distribution of diet specialists and generalists is likely to change towards a major dominance of generalized interactions (some of them newly established interactions) and the loss of specialized reciprocal interactions. The loss of specialized interactions will be observed both at the sink and source communities, independently of the migration scenario considered -preferential migration of large-bodied species or idiosyncratic (figure 1.1c,d). Within closed communities (figure 1.1b), this will result primarily from phenological mismatches mostly affecting specialists. This can have important implications for biodiversity, because specialized interactions, although less frequent than previously expected [111], often result from highly coevolved interactions, and hence it could represent the loss of important evolutionary history. Moreover, some specialized interactions can be crucial for ecosystem functions such as pollination and biological control [219], and the loss of specialized pollinators and parasitoids, respectively, may largely affect ecosystem performance, given the low species redundancy characteristic of specialized interactions (i.e. it is difficult to replace their role by other species).

Source and sink communities, however, will differ in terms of the loss of generalized interactions. We have shown that consumer species with broader diet breadths follow changing climates better than specialists. Thus, source communities will tend to lose generalist consumers (figure 1.1c), whereas sink communities will acquire them (figure 1.1d). It is likely that generalist consumers that migrate will establish new interactions with resources in the sink community not present in the source community they come from. This would result in changes in population dynamics of those resources exploited by the generalist consumer through changes in apparent competition.

Similarly, enemy release of prey as they shift their ranges would trigger dynamic changes. In source communities predators will lose an important prey item (figure 1.1c), while in sink communities new prey species will experience less predation (figure 1.1d). This could eventually lead to increases in population size of new-comers in the community to the detriment of native prey with stronger top-down control, ultimately changing abundance distributions. This, however, could be compensated for if new interactions are established between range-expanding generalist consumers and prey populations that did not interact with each other in the source community.

The third broad pattern is the shift in the distribution of species interaction strengths. In the short term, and in closed communities, warming will strengthen some of the existing interactions (figure 1.1b). However, changes in interaction strengths will be different between source and sink communities if large-bodied species migrate preferentially (figure 1.1c,d). This is based on the scaling of predator-prey interaction strengths with predator-prey body size ratios -the larger the difference in size between predators and prey, the larger their interaction strength [37]. If large-bodied species from high trophic levels and large individuals within a species preferentially migrate, then interaction strengths in the source community would become weaker (loss of large predator-prey size ratios; figure 1.1c in blue) and they would become stronger in the sink community (gain of large predator-prey size ratios; figure 1.1d in blue). This would imply important changes in top-down control and community dynamics across ecosystems as a function of whether they act as source or sink communities of large predators shifting their ranges. This would act in synergy with reported changes in top-down versus bottom-up control in closed ecosystems. Whether bottom-up effects are generally unaffected by warming while top-down effects are strengthened requires further theoretical and empirical exploration (as shown in [234]). Yet, if temperature influences the relative importance of top-down versus bottom-up effects, and large species preferentially migrate, this would have major consequences for community dynamics and species persistence.

Finally, the second major unknown is how the strength of already established interactions will change in the long term, mainly owing to changes in resource availability and accessibility. For example, predators with a diverse prey base might compensate for the smaller size of some of their prey items by shifting their diets to consume a larger proportion of bigger prey, rearranging the distribution of strong and weak interaction strengths within food webs. In addition, it is uncertain how strong interaction strengths among newly interacting species will be, especially in the case of idiosyncratic migration of species irrespective of their body size. Altogether, these uncertainties will render community dynamics within novel ecosystems from climate change a fundamental issue that still needs a solid theoretical and experimental framework.

Chapter 2

Climate change impacts on body size and food web structure on mountain ecosystems

Miguel Lurgi, Bernat C. López, José M. Montoya

Philosophical Transactions of the Royal Society B: Biological Sciences (2012), **367**: 3050–3057

Abstract

The current distribution of climatic conditions will be rearranged on the globe. To survive, species will have to keep pace with climates as they move. Mountains are among the most affected regions owing to both climate and land-use change. Here, we explore the effects of climate change in the vertebrate food web of the Pyrenees. We investigate elevation range expansions between two time-periods illustrative of warming conditions, to assess: (i) the taxonomic composition of range expanders; (ii) changes in food web properties such as the distribution of links per species and community size-structure; and (iii) what are the specific traits of range expanders that set them apart from the other species in the communityin particular, body mass, diet generalism, vulnerability and trophic position within the food web. We found an upward expansion of species at all elevations, which was not even for all taxonomic groups and trophic positions. At low and intermediate elevations, predator : prey mass ratios were significantly reduced. Expanders were larger, had fewer predators and were, in general, more specialists. Our study shows that elevation range expansions as climate warms have important and predictable impacts on the structure and size distribution of food webs across space.

2.1 Introduction

Climate change is expected to be the major threat to biodiversity and one of the main factors affecting human health and well-being in the coming decades [204]. The current distribution of climatic conditions will be rearranged across the globe over the present century [132]. Living organisms must adapt to novel and rapidly changing conditions, and so species must keep pace with climates to survive. Because of differences among species in tracking optimal environmental conditions, climate change will probably have profound effects on community organization and dynamics, as well as on ecosystem functioning [268, 163].

Mountain ecosystems occur on all continents, in all latitudinal zones and within the entire world's main biome types. They support a large portion of the world's biological diversity [126, 134], and are among the most affected and threatened as a result of climate change and population movements [195, 17]. Mountain species with narrow habitat tolerances and/or low dispersal ability are at high risk in the face of climate change [30].

Recent climate change [114] has already impacted biological systems worldwide [193, 225, 192] and has led to significant shifts in the distribution, phenology and behaviour of species [193, 25, 48]. In parallel to latitudinal movements, species inhabiting mountain regions are expected to move upwards to higher, cooler elevations as temperatures rise. Upward movement of alpine plants has already been documented [196], with changes in community composition at high elevations [117]. A median shift of 11.0 m uphill per decade for several plant and animal species has been detected [48, 94].

Different temporal and/or spatial responses of different taxonomic groups can lead to mismatches between interacting species. Spatial mismatches will take place when interacting species shift their ranges at different speeds [268, 163, 48, 61, 32, 128, 122, 264, 144]. Broken and novel interactions resulting from spatial mismatches will probably alter species abundances, distributions and extinction probabilities of species under climate change. However, the question of how climate change will modify community structure and dynamics is still far from being solved [268, 163]. A major challenge is to predict which species will more likely expand their ranges, whether range expanders have particular traits and the consequences of differential range expansions on the structure and dynamics of the food web within which these species are embedded. Because of its fundamental relation to animal metabolism and its role on community organization and food web structure [278, 39, 199, 245], body size can be one of these traits [37]. Other traits that might explain the success of expanding species are linked to their position within the food web [7].

In this chapter, we explore the effects of climate change in the highly diverse vertebrate food web of the south-eastern Pyrenees mountain range. By characterizing the occurrence of elevation range expansions of vertebrate species between two time periods that illustrate climate change, we investigate: (i) the changes in food web properties such as the distribution of links per species, community size-structure and the distribution of predator-prey body mass ratios; (ii) the taxonomic composition of range expanders; and (iii) some characteristics of expanders: body mass, diet breath, vulnerability and trophic position. We do this using data compiled from the literature on habitats, distributions and trophic interactions among species in the Pyrenees.

2.2 Material and methods

We have constructed food webs among vertebrate species combining a unique dataset of species distributions over the southeastern side of the Pyrenees mountain range with observations of their feeding links. The dataset comprises annual presence/absence information of vertebrate species on a geo-spatially located grid, including information on elevation and habitat types observed in each cell of the grid.

The study area includes the southeastern slopes of the Pyrenees (Iberian Peninsula side), from the highest creeks in the centre of the mountain range to the Mediterranean Sea in the east, covering a region of 900,000 ha with elevations between 255 and 3140 m.a.s.l. A climatic dataset was obtained by modelling climatic surfaces from discrete climatic data from the Spanish weather-monitoring system [177, 178, 54]. Climatic variables included temperature ($^\circ$C), precipitation (mm) and the annual and summer precipitation to potential evapotranspiration (PPET) ratio [92]. For the purposes of this work, annual data were aggregated for the elevation ranges considered (see below and appendix 2.A).

Food webs were constructed from existing databases and extensive bibliography search (see appendix 2.A for detailed information about the food web construction). Spatial co-occurrence of species, and hence realized trophic links, were dependent upon three factors: (i) presence in the same grid cell, (ii) elevation and (iii) habitat coincidence. If a pair of species coincided in these criteria and the literature reported a trophic relationship among them, then a link was added to the food web between them. The whole elevation range was divided into three equally distributed elevations: low (from 255 to 1217 m), intermediate (from 1218 to 2179 m) and high elevation (from 2180 to 3140 m). One network for each elevation for each year over the period considered was constructed, resulting in a total of 54 food webs (18 for each elevation). The complete database comprised 253 species (13 mammal carnivores, 40 other mammals, 33 birds of prey, 133 other birds, 10 amphibians, 21 reptiles and three fish species). Temporal variability was studied by comparing two periods, referenced as pre (P1) and post (P2). P1 includes years between 1984 and 1990, both inclusive, and P2 comprises the period between 1991 and 2001 (see figure 2.A.1 in the appendix for an example of built food webs).

We examined the cumulative standardized degree distribution of the networks $P(k > K)$, which describes the fraction of species with a number of links k greater than K, for the P1 and P2 periods at each elevation [64]. Two different cumulative distributions were considered, that of the interactions of species with their predators (standardized outdegree), and the one representing their interactions with their prey or diet breadth (standardized indegree). Two other food web properties were analysed: the standard deviation of generalism (GenSD) and the standard deviation of vulnerability (VulSD).

We compared body mass distribution of newly arrived species over P2 at each elevation range with the body mass distribution of native species at that elevation to assess whether the species expanding their range upwards were larger than the natives. Analyses were carried out for all species together, by taxa (e.g. separating birds and mammals), by separating predator from prey species and by lumping species within trophic levels.

We also calculated the predator-prey mass ratios (PPMR) for all the links present in each web. This value, for each link, was calculated as the base-10 logarithm of the fraction between the body mass of the predator and the body mass of the prey. This allowed for the description of the distribution of these values in each web, and the statistical comparison of these distributions between the P1 and P2 periods.

Statistical analyses included generalized (GLM), mixed and general linear (LM) models, and Student and Kolmogorov-Smirnov tests. All analyses were carried out using R [15, 214].

2.3 Results

2.3.1 Climate

Mean annual temperature increased during the whole period in the three elevation ranges. On average, mean temperature during P1 was significantly lower than during P2 at low and intermediate elevations (see figure 2.A.2 in the appendix), whereas at high elevations, these differences were not significant, although showing the same tendency (table 2.1). On the other hand, neither annual PPET nor summer PPET showed significant differences between P1 and P2 in any of the elevations (see figure 2.A.2 in the appendix).

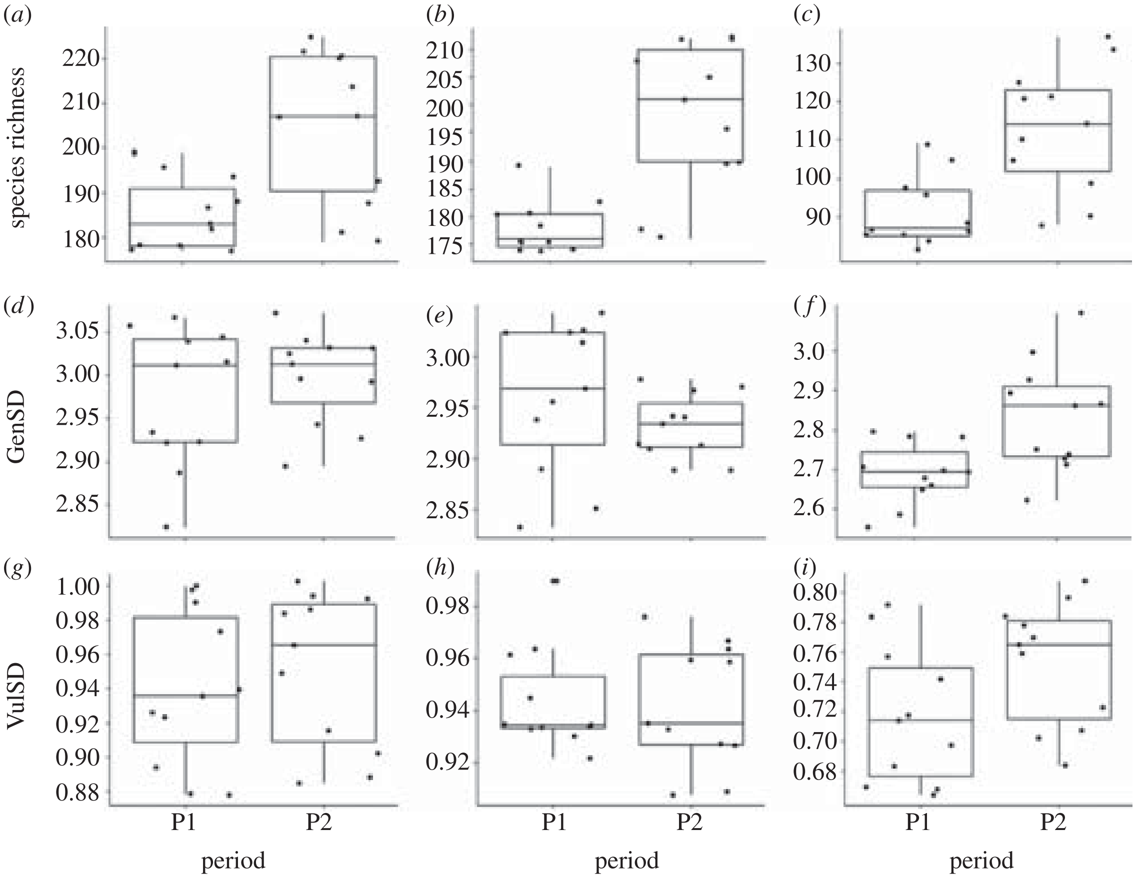


Figure 2.1: Mean values of food web properties at (a,d,g) low, (b,e,h) intermediate and (c,f,i) high elevations during P1 (1984-1990) and P2 (1991-2001) ((a-c) Species richness; (d-f) GenSD; (g-j) VulSD).

2.3.2 Changes in food web properties

(i) Species richness

Low and intermediate elevations showed similar and significantly higher number of species than high elevations (LM, $p < 2.2 \text{ x } 10^{-16}$). At the three elevation ranges, species richness was

	elevation	P1	P2	d.f.: *t*	*p*-value
temperature	low	10.1	10.6	38.8: -3.29	**0.002**
	intermediate	7.1	7.6	37.5: -2.52	**0.016**
	high	3.2	3.6	34.6: -1.54	0.133
species richness	low	186	203	15.7: -2.88	**0.011**
	intermediate	178	197	14.3: -4.25	**0.001**
	high	92	111	17.6: -3.22	**0.005**
GenSD	low	2.98	2.99	14.9: -0.41	0.680
	intermediate	2.96	2.93	11.3: 1.04	0.320
	high	2.68	2.83	17.6: -3.39	**0.003**
VulSD	low	0.95	0.95	19.9: 0.02	0.98
	intermediate	0.94	0.94	19.8: 0.34	0.73
	high	0.72	0.75	19.5: -1.18	0.25

Table 2.1: Comparison of mean annual temperature (°C), species richness (N), standard deviation of generalism (GenSD) and standard deviation of vulnerability (VulSD), between P1 and P2. Significant differences are marked in bold.

significantly higher in P2 than in P1 (table 2.1 and figure 2.1a-c). The number of new species (i.e. those present in P2 but not present in P1) was fairly constant across the entire elevation range (table 2.2). However, at high elevations, they represented a much larger proportion of the natives ($\chi^2 = 17.056, d.f. = 2, p = 0.000019$). Concerning the taxonomical composition of new species, most of them were birds, and within birds, most corresponded to basal species in the food web. It should be noticed, though, that most top predators have large home ranges and are habitat generalists, and thus they were already present at all elevations in P1.

Most new species at each elevation came from lower elevations, indicating elevation range expansions (table 2.3). However, 23 per cent of the new species at low elevations seemed to have moved downwards, going from higher to lower elevations. Thus, 77 per cent and 64 per cent of new species at low and intermediate elevations, respectively, came from the surrounding areas, which, in the Pyrenees, correspond to lower elevations. This percentage was much lower at high elevations, where only 8 per cent of species had moved from the surrounding lowland regions, whereas 92 per cent of the new species were already present at lower elevations within the Pyrenees, either low or intermediate, before 1990.

(ii) Diet generalism

Globally, the GenSD was significantly lower at high than at low and intermediate elevations (LM, $p < 0.0001$). GenSD significantly increased at high elevations from P1 to P2 (figure 2.1f), whereas differences between these two periods at the low and intermediate elevation ranges were not significant (table 2.1 and figure 2.1d-e).

The distribution of the number of prey consumed by each predator (i.e. the standardized indegree distribution) during P1 and P2 was similar at all elevations (figure 2.2a-c). There was a common increase in specialist species, relative to the ones already present. There were slight differences between high elevations and the others, with steeper slopes in the former. However,

group	low elev. ($n = 41$)	intermediate elev. ($n = 40$)	high elev. ($n = 47$)
mammals	7.3	17.5	17
carnivore mammals	7.3	0	4.3
birds	68.3	55	53.2
birds of prey	14.6	20	14.9
reptiles	2.4	2.5	6.4
amphibians	0	5	4.3

Table 2.2: Distribution of new species (percentage) in period P2, according to the taxonomic classification used in this study within each of the three elevation ranges. Low elevation (255-1217 m), intermediate elevation (1218-2179 m), high elevation (2180-3140 m).

	destination		
origin	low elev.	intermediate elev.	high elev.
surrounding	77	64	8
low elevation	-	33	48
intermediate elevation	16	-	44
high elevation	7	3	-

Table 2.3: Percentage of new species at each elevation range and their origin between periods P1 and P2. 'Surrounding' corresponds to species coming from lower elevation surrounding areas. Low elevation (255-1217 m), intermediate elevation (1218-2179 m), high elevation (2180-3140 m).

in all cases, differences of the distributions between P1 and P2 were significant (Kolmogorov-Smirnov test, low elevation: $D = 0.37, p < 0.0001$; intermediate elevations: $D = 0.38, p < 0.0001$; high elevation: $D = 0.28, p < 0.0009$). This, united to the patterns of change observed above for GenSD, indicates that incoming consumer species at the high elevation range were more generalists -i.e. had broader diet breadths- than native consumers.

(iii) Vulnerability

The VulSD was significantly lower at high than at low and intermediate elevations (LM, $p < 0.0001$). VulSD did not change between P1 and P2 (figure 2.1g-i). This suggests that within an elevation range, predation pressure was equally distributed among prey species in the food web, and this did not change with changing climatic conditions and/or the arrival of new species.

Marked differences occurred, however, when comparing the number of predators attacking new and native prey between P1 and P2 (figure 2.2d-f). At all elevations, new prey species were exposed to fewer predators than their native counterparts ($D = 0.30, p < 0.0001$; $D = 0.35, p < 0.0001$; and $D = 0.38, p < 0.0001$, at low, intermediate and high elevations, respectively), as shown by steeper standardized outdegree distribution slopes for P2.

2.3.3 Size-structure: predator-prey mass ratios

We compared the distribution of PPMR in the native food web (P1) with the distribution of mass ratios only considering newcomers at P2 and their interaction with natives. At the three elevations, PPMRs at P1 were significantly higher, although only marginal at high elevations ($p < 0.0001$ at low and intermediate elevations, and $p = 0.06$ at high elevation) than at P2, indicating either an increase of big prey and/or a decrease of big predators from P1 to P2 (figure 2.3a-c). The same result was obtained when only basal species and their predators were considered, with significant differences at high elevations as well ($p < 0.0001$, $p < 0.001$ and $p = 0.047$ at low, intermediate and high elevations, respectively). The analysis of the body mass of new species (see table 2.A.2 in the appendix) revealed that incoming basal species were generally larger, and thus the differences in PPMRs were likely due to an increase of big prey instead of a decrease of predator sizes.

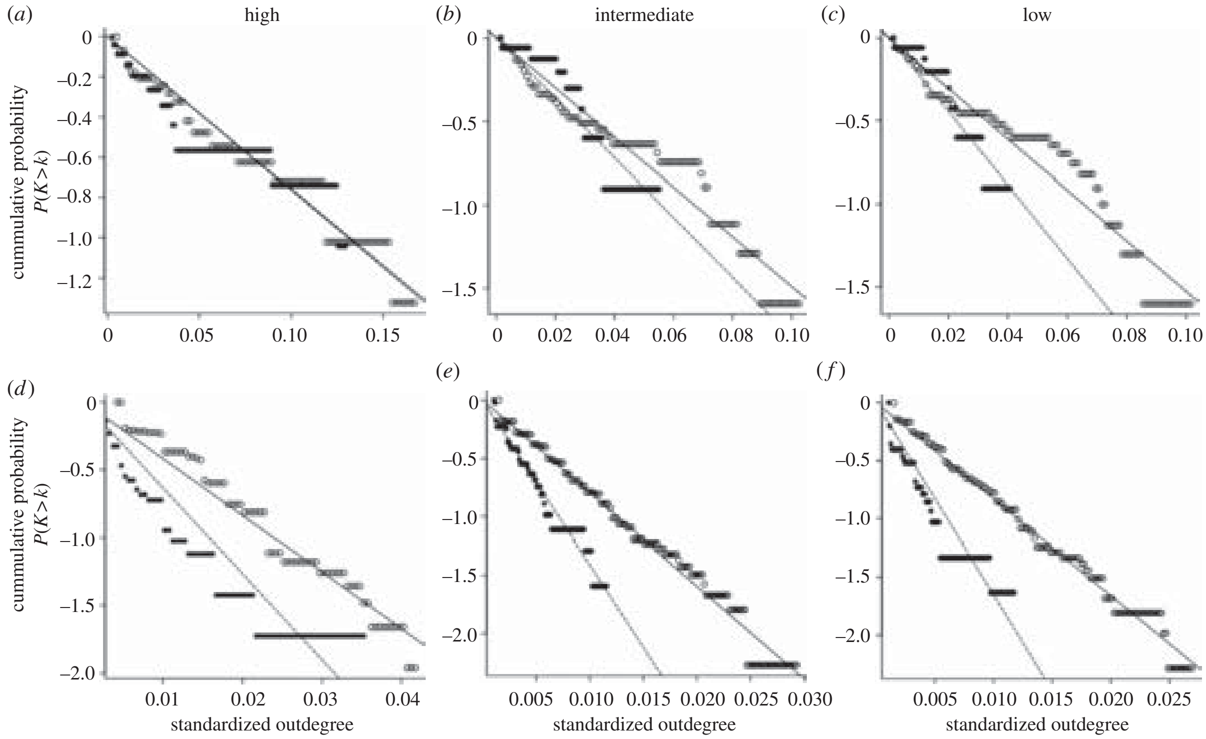


Figure 2.2: Cumulative probability distributions of the standardized indegree -number of prey species each predator feeds upon (a-c)- and the standardized outdegree -number of predators attacking each prey (d-f)- at each elevation range during the periods P1 (open circles, 1984-1990) and P2 (asterisks, 1990-2001).

2.3.4 Expanders versus non-expanders: species traits

(i) Habitat generalism

Contrary to previous observations and expectations [57], expanders at intermediate and high elevations were not more habitat generalists than the natives at that elevation. A significant example is provided by incoming bird species at high elevations: they were more habitat specialists than native birds, occupying about half of the suitable habitats, regardless of their trophic level (see table 2.A.3 in the appendix).

(ii) Trophic relations

The mean standardized outdegree values of expanders were significantly lower than those of non-expanders, indicating that expanding species had few predators (both at the native and at the new elevation; table 2.1). On the other hand, we found no significant differences of the mean standardized indegree values between expanders and non-expanders for the whole period (table 2.1).

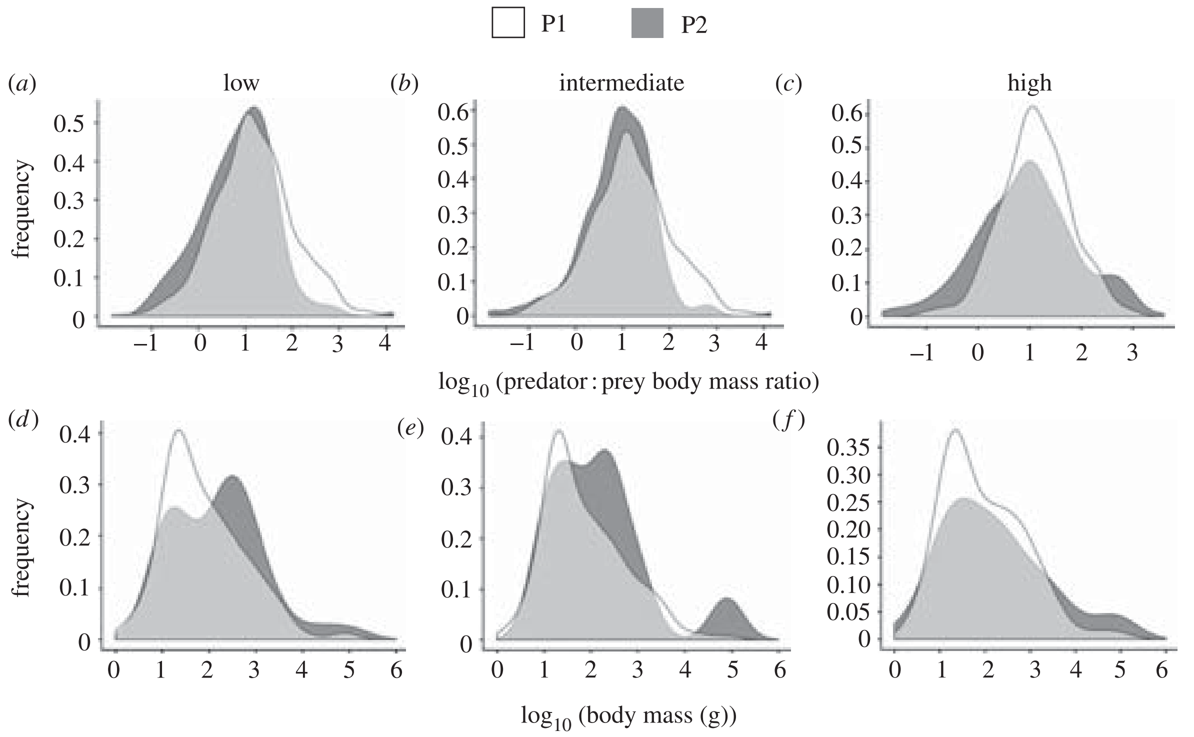


Figure 2.3: (a-c) Comparison of PPMR probability distribution of the food webs from P1 (1984-1990) and the food webs from P2 (1991-2001) at each elevation range; (d-f) Comparison of body mass probability distribution of new prey incomers in the period P2 (1991-2001) and native prey species already present in P1 (1984-1990) at each elevation range.

(iii) Body mass of expanders

New prey species were significantly larger than natives at low and intermediate elevations ($p = 0.04$ and $p = 0.02$, respectively; figure 2.3d-e), whereas incoming prey at high elevations were not significantly larger than the natives (figure 2.3f). Observed differences at low and intermediate elevations were mostly due to range expanding birds, whereas differences in body mass between newcomers and natives were not observed for mammals and carnivores (see table 2.A.2 in the appendix). On the other hand, new predators at any elevation range were not larger than native predators, and hence predator body mass was not a good predictor of elevation range expansion in our data.

2.4 Discussion

We show that mountain ecosystems are experiencing important changes in species composition, food web structure and community size distributions. Novel communities resulting from climate change are characterised by a higher proportion of larger basal prey species. We observed an upward expansion of species across the whole elevation range, with most expanders representing birds from low trophic positions. At low and intermediate elevations, new basal species were larger than native species, promoting significant changes in PPMR. At the highest elevations, new species were not larger than the natives, were more habitat specialists and, among the expanders, were the ones with more similar diet breadths than the natives. At all elevations, expanders experienced an important enemy release and were attacked by fewer predators than natives.

Species richness increase paralleled that of mean temperature, but different changes across elevations are manifested by other network metrics. At low and intermediate elevations, neither GenSD nor VulSD increased with temperature, and both temperature and GenSD increased at high elevation, with new incoming species having broader diets than the natives. This increase in species richness supports the idea that, despite climate change being expected to reduce the number of species globally, species richness can increase locally [250, 159]. At least at our temporal resolution, extinctions have not occurred, supporting findings that state that the mechanisms that cause climate-induced extinctions are not instantaneous [193, 211, 75, 275, 194, 98].

There is increasing evidence that different taxonomic groups show different elevation responses to changing climatic conditions [32, 18]. Most expanders were prey species down in the food web, mostly birds. This contrasts with other studies [48] showing that birds responded least in terms of elevation shifts than other taxonomic groups. Most basal species in our food webs reproduce annually, have a diet is based on insects and/or plants, and share most predators. But birds might be more mobile than small mammals [231], and their responses to warming include the establishment of introduced species outside their endemic climatic ranges [57, 240, 53].

Expanders are species visiting new environments, and may survive if they find a suitable habitat, they find enough resources and/or predation pressure is not too strong. Expanders did not have wider diet breadths than non-expanders, but they were larger and were attacked by fewer predators. The first pattern disagrees with studies stating that more generalist consumers are good candidates to firstly move upwards [144, 18, 233]. Actually, specialists are considered particularly vulnerable to extinction as a result of environmental change [233, 155, 113, 35]. The lack of inequality found can be a consequence of living in an extreme and extremely fluctuating habitat, with species forcedly adapted to a relatively highly diverse diet. More diet breath can be a good predictor only for certain taxonomic groups [7].

Concerning the effects of predators, expanders had significantly fewer predators than non-expanders (mean values of 2.2 versus 3.9, respectively). This agrees with the enemy-release hypothesis. A species with few predators expanding its range is likely to find new environments with no or fewer predators, and so the establishment in this new habitat has more probabilities of success.

The analyses of standardized indegree and outdegree distributions support these results and provide an additional dimension. Our results show that consumers with relatively wide but lower diet breaths than native species and, more importantly, with a lower predation pressure, are the best suited to expand their ranges. Expanders were also more habitat specialists. As for diet breath, the explanation might rely on environmental conditions. Some species that live at the highest elevations have adaptations to cope with different environmental conditions in winter and summer. For instance, many of them make seasonal elevation migrations, and so they must be habitat generalists to some extent to survive in a completely different environment. Incoming species should not need to have these pre-adaptations to extremely changing environments, and so they do not need to be such habitat generalists. An alternative or complementary explanation is based on the fact that specialists are more efficient in exploiting resources than generalists.

So, a relatively more specialist -but still quite generalist- species could be favoured in new environments.

Basal expanders had significantly larger body sizes than non-expanders. While warming generally reduces body size within local communities [233, 56, 84], it is not clear whether large body-sized species tend to shift or expand their ranges more easily than smaller ones [144]. It is worth noting that species at higher trophic positions were homogeneously distributed across elevations; so range expansions in these groups would not occur.

The decrease of PPMR at low and intermediate elevations was due to larger prey species moving upwards. This might have important dynamic consequences. PPMR are proxies of interaction strengths, mostly in aquatic food webs [19], ultimately determining food web dynamics. If smaller body mass ratios imply weaker interaction strengths, we should expect mountain ecosystems to be less top-down controlled in the near future. The reported mechanisms behind loss of top-down control in our study differs from those reported in [110].

The complexity of the food web analyses presented here, expanding many years to detect evidence in natural systems of climate change effects, requires an alternative way of building the food web (see [279] for a similar approach). Because interactions cannot be directly assessed in such food webs due to the impracticability of determining the diet of all species at each altitude each year, all feeding interactions come from aggregating individual species diets, and do not change over time unless the two interacting partners do not co-occur in a given habitat at a given elevation in a given year. Our approach, for example, does not allow for dietary shifts of expanders into their new environments. However, our database includes all found interactions at different environments and elevations; so it covers a wide range of species. Hence, it is unlikely, but possible, that a new potential interaction between a range consumer and a native resource is not already contemplated in our database.

2.5 Conclusions

The Pyrenees are showing some responses to climate change that could be representative of what is happening in other mountain ecosystems worldwide, i.e. the appearance of communities with novel species combinations. These novel communities are characterized by a higher proportion of larger basal prey species, mostly birds. The evidence that most incoming species come from lower elevations clearly indicates that, in the long term, if climate change continues at a similar rate, the vertebrate community at the highest elevations will become more similar to that at lower elevations. If range contractions occur at low elevations [279], and inhabiting species at the highest elevations are forced to move upwards, species extinctions in mountain environments are likely to occur in the intermediate-long term. Our study suggests that the level of climate warming that has already taken place in the Pyrenees is sufficient to have also generated changes in its size-structure and food web properties, which could have profound impacts on community dynamics, biodiversity maintenance and ecosystem functioning. Alpine communities are likely to keep changing in the next decades or centuries, probably exacerbating the patterns of change reported here.

Appendix

2.A Materials and methods

2.A.1 Study region - climate

The climate in this region is subject to Atlantic and Mediterranean influences and the effect of macrorelief on precipitation and temperature. In these mountains, annual precipitation exceeds 600 mm and sometimes reaches 2000 mm at the highest divides [136]. Most of the annual precipitation falls during spring and autumn. Summers are generally relatively dry, with the annual 0 °C isotherm located at 2726 masl [59], and above 1600 masl, with most of the precipitation falling as snow during the cold season (November-May). Since the beginning of the 20th century, and particularly since the 1960s, most of the cultivated areas in the Pyrenees have been abandoned, becoming replaced by dense shrubs and young forests [260]. Climate change effects have been reported in the Pyrenees, particularly in terms of snowfall and snow accumulation [135].

A climatic data set was obtained by modelling climatic surfaces from discrete climatic data from the Spanish weather-monitoring system. All weather stations in the region with available data were included in the analysis. The time period was limited to January 1970-December 2010. Multiple regressions with residual correction, together with spatial interpolation based on inverse distance weighting and splines, were used to predict minimum, maximum, and mean temperature with a spatial resolution of 180 m [177, 178]. The procedure was implemented in a Geographic Information System environment. The explanatory variables were elevation, latitude, continentality (linear distance to Mediterranean and Atlantic coasts), potential solar radiation, and terrain curvature - all derived from a digital elevation model. A fraction of the used stations (40%) was not included in the development of the model and was used only afterwards for cross validation purposes, giving errors that are comparable with those obtained by current climatic-mapping efforts using spatial interpolation tools [177, 178, 54]. Monthly potential evapotranspiration (PET) was calculated from monthly values of minimum, maximum, and mean temperature using the Hargreaves-Samani method [92]. The average (1970-2010) values of mean annual temperature, annual PET, and the average ratio of precipitation (P) to PET for June-August (summer P/PET, a measure of summer drought stress) were used to characterize the climate of each cell. For the purposes of this work, data were aggregated for the elevation ranges considered (see below).

2.A.2 Species presence assessment

The Biodiversity Data Bank of Catalonia (BDBC, http://biodiver.bio.ub.es/biocat/), centralises all the information of plant and animal citations in Catalonia. Information is stored spatially ex-

Habitat	**Low elevation (%)**	**Intermediate elev.** (%)	**High elev. (%)**
Small glaciers	0.0	0.0	0.3
Water	1.0	0.2	2.8
Urban	2.1	0.5	0
Deciduous Forests	12.8	5.1	0.0
Conifer forests	26.8	41.0	1.3
Agricultural fields	14.6	1.4	0.0
Sclerophilous forests	10.8	0.6	0.0
Forest plantations	0.0	0.7	0.0
Riparian vegetation	0.8	0.0	0.0
Shrubland	6.3	16.8	0.0
Mixed forests	5.2	1.4	0.0
Alpine swamps	0.0	0.2	0.0
Meadows	16.4	28.9	48.0
Rocky habitats	3.1	3.3	47.0

Table 2.A.1: Distribution of habitats within the three elevational ranges in the Catalan Pyrenees considered in this chapter. Low Elev. (255-1217m), Intermediate Elev. (1218-2179 m), High Elev. (2180-3140 m).

plicitly, at 10x10 km resolution, and includes the presence of a species and the year the species is observed. No information on population densities is provided in the database. The information in the BDBC was complemented with the database of the Catalan Institute of Ornithology (http://www.ornitologia.org/ca/), and several atlases for mammals, reptiles and amphibians, all at the 10x10 km resolution. A database of species distribution was obtained for the 1970-2010 time period. However, in this work we use only data from 1984 to 2001, due to low quality of some data before 1984 and after 2001.

2.A.3 Map of habitats

Habitats were extracted from the cartography of habitats of Catalonia at a resolution of 1:50.000, where the thematic elements are the habitats created from the most abundant plant species available in the BDBC. In this cartography, the minimum area represented is of 1 ha, and each polygon can be assigned to the 3 most represented habitats within and the percentage of surface that each of them covers. Each habitat is identified by a code, according to a legend created specifically for this work and may correspond to one or more CORINE habitats. A total of 33 different habitats according to their composition and most representative species were identified.

Because we were interested in looking at the elevation shifts of species, the whole elevation range found in the study area was divided into 3 equally distributed elevations: low (from 255 to 1217 m), intermediate (from 1218 to 2179 m) and high elevation (from 2180 to 3140 m). The 33 habitats were grouped into 14 categories to determine their presence at each elevation (table 2.A.1). The Shannon diversity index for habitat types decreased with elevation, indicating a reduction in both habitat types and equitability (H=2.0, 1.5, and 0.9 at low, intermediate, and high elevations respectively). All habitats were relatively equally represented at low elevations, while intermediate elevations were dominated by coniferous forests (41%), meadows (28%) and shrubland (16%); high elevations were dominated by meadows (48%) and rocky habitats (47%).

2.A.4 Construction of the annual food webs

The presence/absence information of species on each 10x10 km cell of the geographical grid was accompanied by species-specific features including the habitats in which each species lives, its maximum body mass, and taxonomic group (reptiles, amphibians, birds, birds of prey, mammals and carnivore mammals). Body masses were obtained from an exhaustive search in the literature for all species present in the database. Fish, invertebrates, carrion and primary producers were not resolved to the species level, and were not considered in our analyses. Because of this, species that are typical from the second trophic level are referred to throughout the text as basal (e.g. passerine birds). For each year and cell, an elevation range for each species was assigned according to the maximum and minimum elevations of all habitats (among the 33 categories) suitable for that species present at that cell. For example, for a given cell C with habitats (A, B, F, G) inside, and a species X able to live in habitats (A, B and E): if X is present in C, then the minimum and maximum elevations for species X in cell C would be the min value between the minimum elevations of habitats A and B in cell C, and the max value between the maximum elevations of habitats A and B in cell C, respectively.

Trophic interactions were extracted from an exhaustive literature review, describing the whole set of known trophic links among the species in our database. Only interactions at the species level were included. The total database of interactions included 2676 interactions coming from a variety of empirical studies, including gut content analyses, fecal analyses, direct observations, rest analyses from bird nests or mammal burrows, and pellet analyses. Only in some exceptional cases, expert knowledge assessment was used to verify and/or complete some data.

In summary, co-occurrence of species, and hence realised trophic links, were dependent upon three factors: (i) grid cell, (ii) elevation and (iii) habitat. If a pair of species coincided in these criteria, and the literature reported a trophic relationship among them, then a link was added to the food web between them. One network for each elevation for each year over the period considered was constructed, resulting in a total of 54 food webs (18 for each elevation). The complete database comprised 253 species (13 mammall carnivores, 40 other mammals, 33 birds of prey, 133 other birds, 10 amphibians, 21 reptiles and 3 fish species).

2.A.5 Temporal variability in food webs and elevation range expansions

We were interested in the temporal change of species composition, community size-structure and food web properties at each elevation, and the extent to which these changes were a consequence of species range expansions across elevations triggered by climate change.

Temporal variability was studied by comparing two periods, referenced as pre (P1) and post (P2). P1 includes years between 1984 and 1990, both inclusive, and P2 comprises the period between 1991 and 2001. The year 1990 was chosen as the separation between the pre and post periods because it was the exact mid-point of our original climatic dataset, which ranged from 1970 to 2010. Since the choice of the separation between the pre and post periods was to a certain extent arbitrary, we performed additional analyses taking a different year for separation (1992). We did not observe any significant differences on any of the results presented here. For simplicity, we only show results using 1990 as the separation between P1 and P2.

Food web topology and community size-structure were characterized at each elevation before and after 1990. We then looked at food webs from the same elevation and different periods and obtained the set of species that were present on P1 and the set of species newly incorporated into the network during P2. The origin of the newcomers during P2 was also analysed to assess the extent to which species in the Pyrenees are expanding their elevation ranges and what are the consequences of this to food web structure. Fig 1 shows an example of the networks of year 2000 at the three elevation ranges, highlighting new species only observed at P2.

2.A.6 Food web properties

A food web is here defined as an adjacency matrix **A** describing the trophic interactions between the S species in the community:

$$\mathbf{A} = [a_{ij}]_{SXS}$$

where a_{ij}=1 if prey *i* is attacked by predator *j*, and a_{ij}=0 otherwise. This matrix has *L* nonzero elements (a_{ij}) wherever a trophic interaction is observed between a pair of species, and k_i interactions per species.

We examined the cumulative standardised degree distribution of the networks $P(k > K)$, which describes the fraction of species with a number of links *k* greater than *K*, for the P1 and P2 periods at each elevation. The standardised degree is calculated as the degree of a species divided by the total number of links in the food web [272]. Two different cumulative distributions were considered, that of the interactions of species with their predators (standardised outdegree), and the one representing their interactions with their prey or diet breadth (standardised indegree). These distributions describe the probability with which we can expect to find a species in the food web with a given number of predator species, and with a given number of preys, respectively.

Two other food web properties were analysed: the standard deviation of generalism (GenSD) and the standard deviation of vulnerability (VulSD). These quantify the variability of species' normalized prey (G_i) and predator (V_i) counts, respectively:

$$G_i = \frac{1}{L/S} \mathop{}\limits_{j=1}^{S} a_{ji} \quad , \quad V_i = \frac{1}{L/S} \mathop{}\limits_{j=1}^{S} a_{ij}$$

where L, S and a_{ij} are defined as above. Normalizing with L/S makes standard deviations comparable across different webs by forcing mean G_i and V_i to equal 1 [272]. These measures (GenSD and VulSD) quantify the variability in terms of numbers of prey and predators among the species in the food web.

2.A.7 Body mass distributions and predator:prey mass ratios

We compared body mass distribution of newly arrived species over P2 at each elevation range with the body mass distribution of native species at that elevation to assess whether the species expanding their range upwards were larger than the natives. Analyses were carried out for all species together, by taxa (e.g. separating birds and mammals), by separating predator from prey species, and by lumping species within trophic levels.

We also calculated the predator-prey mass ratios (PPMR) for all the links present in each web. This value, for each link, was calculated as the base-10 logarithm of the fraction between the body mass of the predator and the body mass of the prey. This allowed for the description of the distribution of these values in each web and the statistical comparison of these distributions between the P1 and P2 periods.

2.A.8 Statistical analyses

All variables defined above were analysed for each food web and/or time period: species richness, indegree and outdegree cumulative distributions, body mass and predator:prey mass ratio distributions, standard deviation of generalism, and standard deviation of vulnerability. In addition, the incoming species at each elevation range and their characteristics were also considered in the analyses. Statistical analyses included generalised (GLM), mixed (lme4 package [15]), and general linear (LM) models, and Student and Kolmogorov-Smirnov tests. To analyse the differences between expanders and non-expanders, generalized models were used, either using group as a random factor (mixed models) or not. In both cases, the response variable was binary, and the explanatory variables were all species characteristics considered (standardised indegree, standardised outdegreee and log10(body mass)). All analyses were performed using R [214].

Sps	Trophic level	Origin	Destination	*p-value*	Bigger?
All	All	S	Low	0.0226	yes
All	All	S	Interm.	0.0155	yes
Birds	All	S	Low	0.0395	yes
Birds	All	S	Interm.	0.0176	yes
Mammals	All	Low	Interm.	0.0582	yes
All	0	S	Low	0.0221	yes
All	0	S	Interm.	0.0071	yes
All	0	Low	Interm.	0.0304	yes
Birds	0	S	Low	0.00317	yes
Birds	0	S	Interm.	0.00094	yes
Mammals	0	Low	Interm.	0.03	yes

Table 2.A.2: Comparision between body mass of the incoming species and the natives between peeriods P1 and P2. Only significant results are shown. 'S' corresponds to species coming from lower altitude surrounding areas. 'Bigger?' indicates whether incoming species are bigger than the natives or not.

Group	TL	Origin	Destination	*p-value*	Mean pre	Mean post
All	All	Low	High	0.086	19	15
Birds	All	Low	High	0.002	23	15
Birds	All	Interm.	High	0.022	24	16
Birds	0	Low	High	0.019	22	15
Birds	0	Interm.	High	0.060	22	15
Birds	1-2-3	Low	High	0.007	30	13
Birds	1-2-3	Interm.	High	0.025	30	15

Table 2.A.3: Comparison of the number of suitable habitats between the incoming species and the natives. Only comparisons with significant differences are shown. Group: taxonomic group; TL: trophic level; Origin and Destinations: elevation ranges; 'Mean pre' and 'Mean post' indicate the average of suitable habitats of the natives and the incoming species.

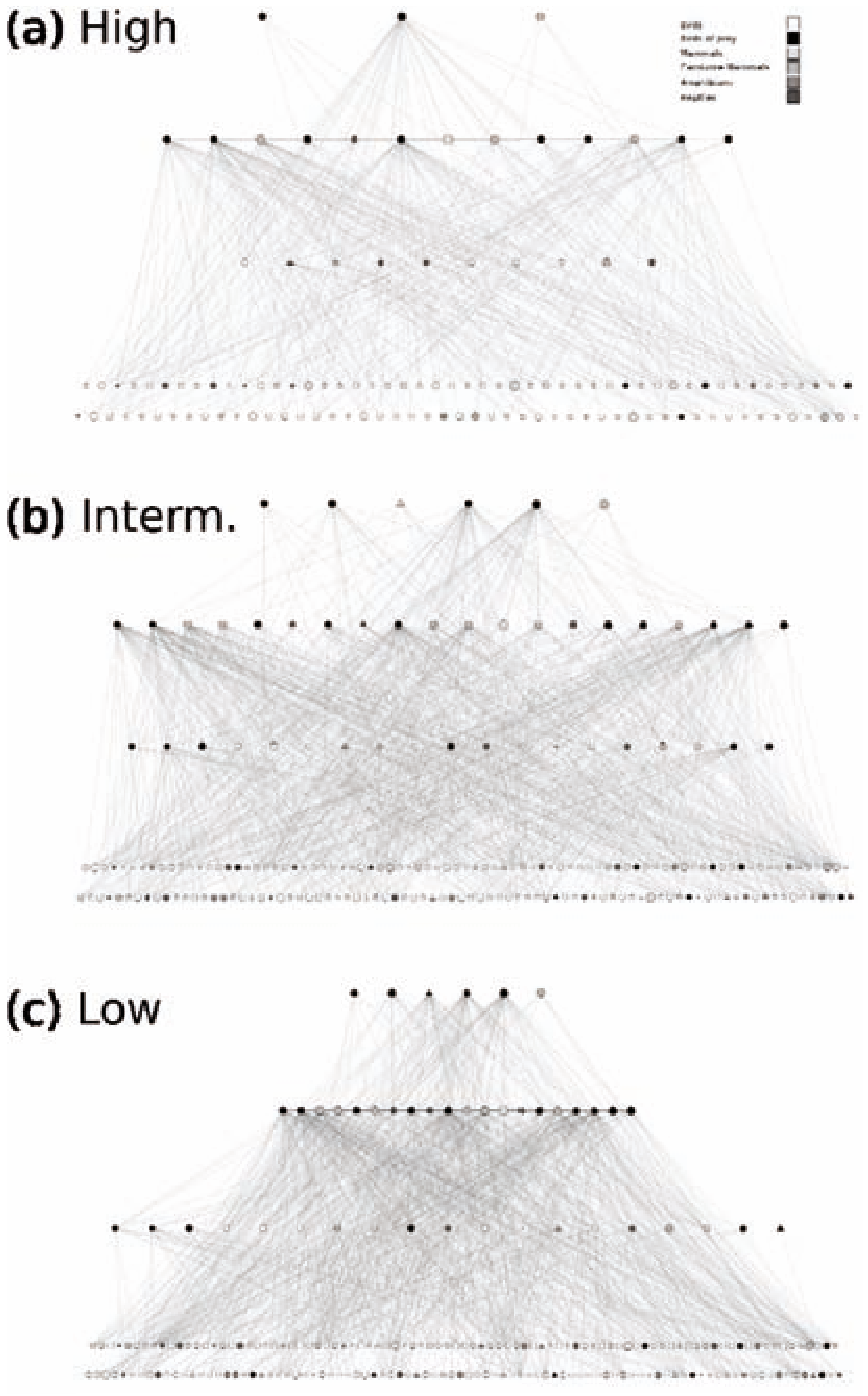


Figure 2.A.1: Food webs corresponding to year 2001 at low, intermediate and high elevations. Each circle corresponds to a taxonomic species, and links indicate a trophic relationship. Circle diameter is the log10 of species body size. Triangles indicate new species at P2 (1991-2001) that were not present at P1 (1984-1990).

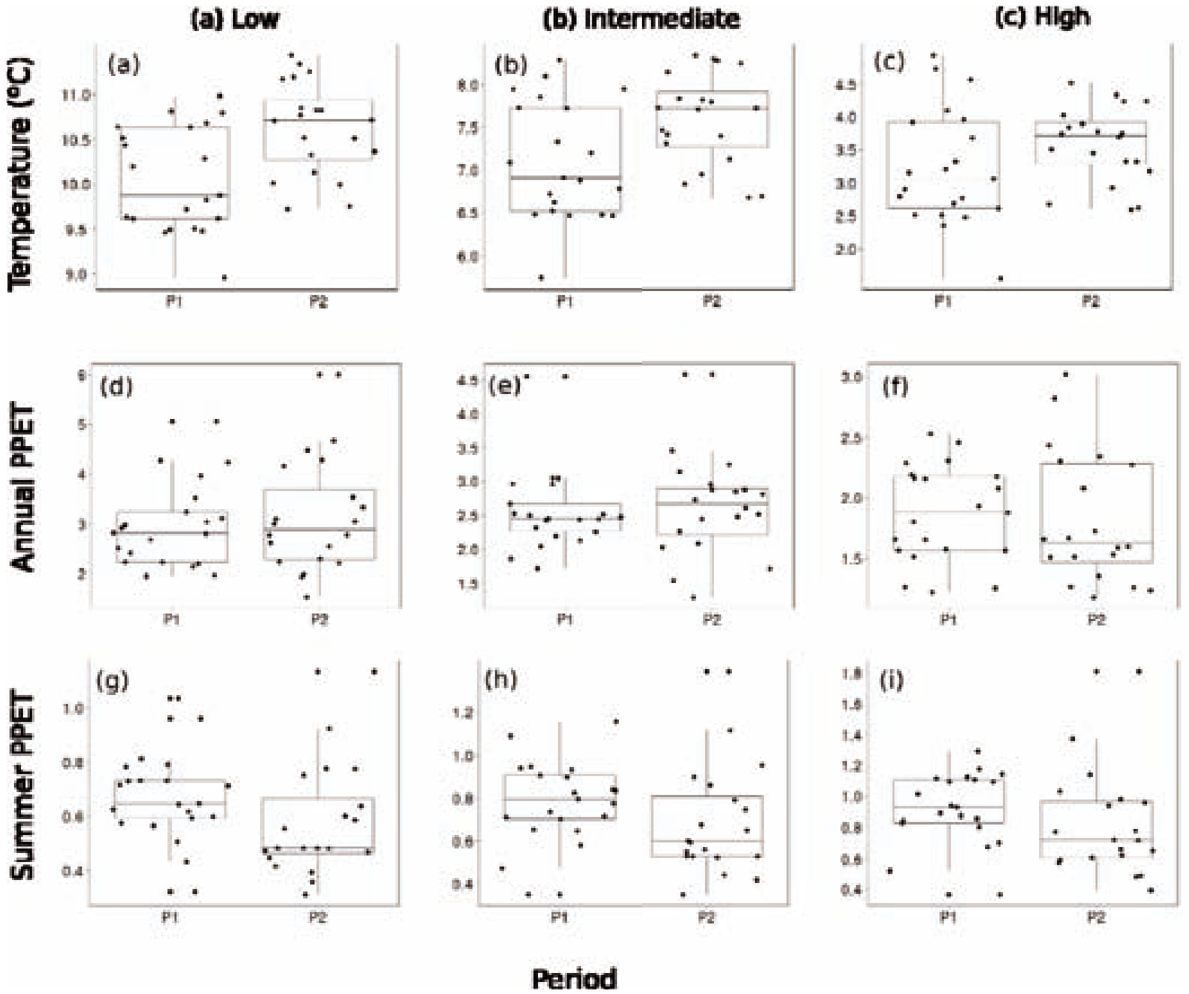


Figure 2.A.2: Mean annual Temperature, Annual and Summer PPET at each elevation range during the periods P1 (1984-1990) and P2 (1991-2001).

Chapter 3

On the dimensionality of ecological stability

Ian Donohue, Owen L. Petchey, José M. Montoya, Andrew L. Jackson, Luke McNally, Mafalda Viana, Kevin Healy, Miguel Lurgi, Nessa E. O Connor, Mark C. Emmerson

Ecology Letters (2013), **16**(4): 421–429

Abstract

Ecological stability is touted as a complex and multifaceted concept, including components such as variability, resistance, resilience, persistence and robustness. Even though a complete appreciation of the effects of perturbations on ecosystems requires the simultaneous measurement of these multiple components of stability, most ecological research has focused on one or a few of those components analysed in isolation. Here, we present a new view of ecological stability that recognises explicitly the non-independence of components of stability. This provides an approach for simplifying the concept of stability. We illustrate the concept and approach using results from a field experiment, and show that the effective dimensionality of ecological stability is considerably lower than if the various components of stability were unrelated. However, strong perturbations can modify, and even decouple, relationships among individual components of stability. Thus, perturbations not only increase the dimensionality of stability but they can also alter the relationships among components of stability in different ways. Studies that focus on single forms of stability in isolation therefore risk underestimating significantly the potential of perturbations to destabilise ecosystems. In contrast, application of the multidimensional stability framework that we propose gives a far richer understanding of how communities respond to perturbations.

3.1 Introduction

Understanding the factors that determine the stability of biological communities has been a focal point of ecological research for decades (e.g. [146, 149, 202, 151, 162, 106, 3]). One challenging aspect of stability is its many components, including asymptotic stability, resilience, resistance, robustness, persistence and variability (table 3.1; [202, 107]). Thus, ecological stability is touted as a multifaceted and complex concept [190, 202, 106]. This perception has been compounded by the propagation of a wide variety of terms for describing similar aspects of stability [202, 89]. Progress in the field has been hampered further by a lack of comparability among studies and a disparity between the components of stability that most frequently comprise the focus of either theoretical or empirical studies. The former tend to concen- trate on mathematical asymptotic stability [150, 202, 3]; a binary measure (communities are either stable or unstable at an equilibrium point) which itself has many forms [133]. On the other hand, empirical studies typically measure the temporal variability of some aggregate feature of populations or communities (typically as the coefficient of variation of their biomass or abundance; e.g. [242, 252]; table 3.1) to characterise their stability.

In spite of its multidimensionality, the few studies that measured multiple components of ecological stability simultaneously considered them as independent and therefore analysed them separately (e.g. [83, 185]). It is likely, however, that components of stability are related [93, 202]. For example, communities with high temporal variability in abundance are expected to have low robustness (the number of secondary extinctions caused by the initial loss of a species; table 3.1) due to an increased extinction risk in species with small population sizes [208, 127]. Theoretical research [93] has also suggested that pairwise relationships between components of stability could vary; the resistance of populations to perturbations (the magnitude of change in their abundance or biomass in response to a perturbation; table 3.1) may correlate either positively or negatively with their resilience [the length of time taken to return to their pre-disturbance state, also referred to as ‘elasticity’ (e.g. [190])], depending on the nature of intrinsic population growth rates and their sensitivity to the environment. However, remarkably little is known about the form or strength of correlations among multiple components of ecological stability, or the potential causes or consequences of those relationships. That is, there is no general framework that integrates across the different dimensions of stability.

The primary question about multidimensional ecological stability is how correlated or independent are the various components of stability (Box 1)? Few and weak correlations among stability components (Box 1a) imply that simultaneous quantification of multiple components of stability is necessary and suggests that different processes and mechanisms could be responsible for different components of stability. Alternatively, many strong correlations among several components of stability (Box 1b, c, d) imply that the effective dimensionality of ecological stability is low. This makes ecological stability less complex than if correlations were weak. Finding strong correlations (i.e. low effective dimensionality) implies that similar processes and mechanisms underlie multiple components of ecological stability and/or that there are causal connections among components of stability.

Measure of stability	Description	Method of quantification
Variability (temporal and spatial)	The variability of community biomass or, less frequently, abundance in time or space [52, 106]. Higher variability equates to reduced stability.	***Temporal variability***: quantified as the coefficient of variation (CV; standard deviation divided by the mean, expressed as a percentage) of total algal cover (e.g. [202, 252, 185]) in experimental plots over time. To test whether our measures of variability were confounded with any particular positive or negative shifts in algal cover over the duration of the experiment, which may be caused by, for example, transient dynamics or seasonality, we detrended variability in total algal cover (see [252]). This was done by deriving the standard deviation of the residuals from the linear regression of total algal cover of each plot on month and dividing this by the respective mean total algal cover to obtain the detrended community-level temporal CV. ***Spatial variability***: quantified as the CV of total algal cover (e.g. [202, 252, 185]) in experimental plots in space. The CV of algal cover in space (spatial CV) was quantified from measurements of total algal cover among the plots within each experimental treatment on each census. We detrended spatial variability in total algal cover by deriving the standard deviation of the residuals from the linear regression of total algal cover of plots within treatments on month and dividing this by the respective mean total algal cover to obtain the detrended community-level spatial CV.
Compositional turnover	The extent of change in community composition over time, thus integrating elements of invasions, extinctions, resistance and variability. The reciprocal of persistence ([202]). Less stable communities experience higher rates of compositional turnover.	Quantified for each experimental plot as the Jaccard similarity in algal community composition (calculated from species presence/absence data) between consecutive surveys (after the commencement of experimental manipulation).
Number of extinctions (robustness)	Corresponds to the number of secondary extinctions caused by the initial loss of a species. Sometimes referred to as structural robustness [238, 72, 2, 70].	Quantified for each plot as the number of algal taxa that were observed in plots prior to experimental manipulation but were absent at the end of the experiment.
Number of invasions	Based on the concept of persistence. Communities that are more difficult to invade are more persistent and vice versa ([202]).	Quantified for each plot as the number of algal taxa that were observed in plots at the end of the experiment but were absent prior to experimental manipulation.
Resistance	The extent of change in community structure caused by a perturbation ([202]). Corresponds to MacArthur's [146] definition of 'stability'. Also referred to as 'inertia' by Orians [190]. More resistant communities show less structural change.	Measured as the inverse of the Euclidian distance from each experimental plot to the centroid of the unmanipulated uncaged treatment at the end of the experiment (based on Bray-Curtis similarity matrices calculated from log (x+1)-transformed algal cover data). This provides a holistic measure of the extent of change in algal community structure over the duration of the experiment, over and above natural background dynamics. The resistance of the caged plots with no experimental consumer removals did not differ statistically from the inverse of the distance of the uncaged plots to their treatment centroid ($t_3 = 0.24$, $P = 0.82$).

Table 3.1: Description of our measures of stability, based primarily on the definitions of Pimm [202].

A second question about multidimensional stability is whether the effective dimensionality of stability changes in the face of major perturbations, such as biodiversity loss. This could be explored, for example, by simulating the loss of different predator species and their prey both separately and together (figure 3.1), with a focus on consumer species conceivably capturing effects most realistically because species at higher trophic levels tend to suffer higher extinction rates [67] and exert disproportionately large effects on the structure and functioning of ecosystems [191, 160, 77]. The loss of different functional groups of consumers may also trigger shifts in the relationships among different components of ecological stability. For example, empirical studies have shown that predators are key contributors to ecosystem robustness [191, 247, 77], whereas intermediate consumers such as grazers can regulate the spatial variability of their prey [99].

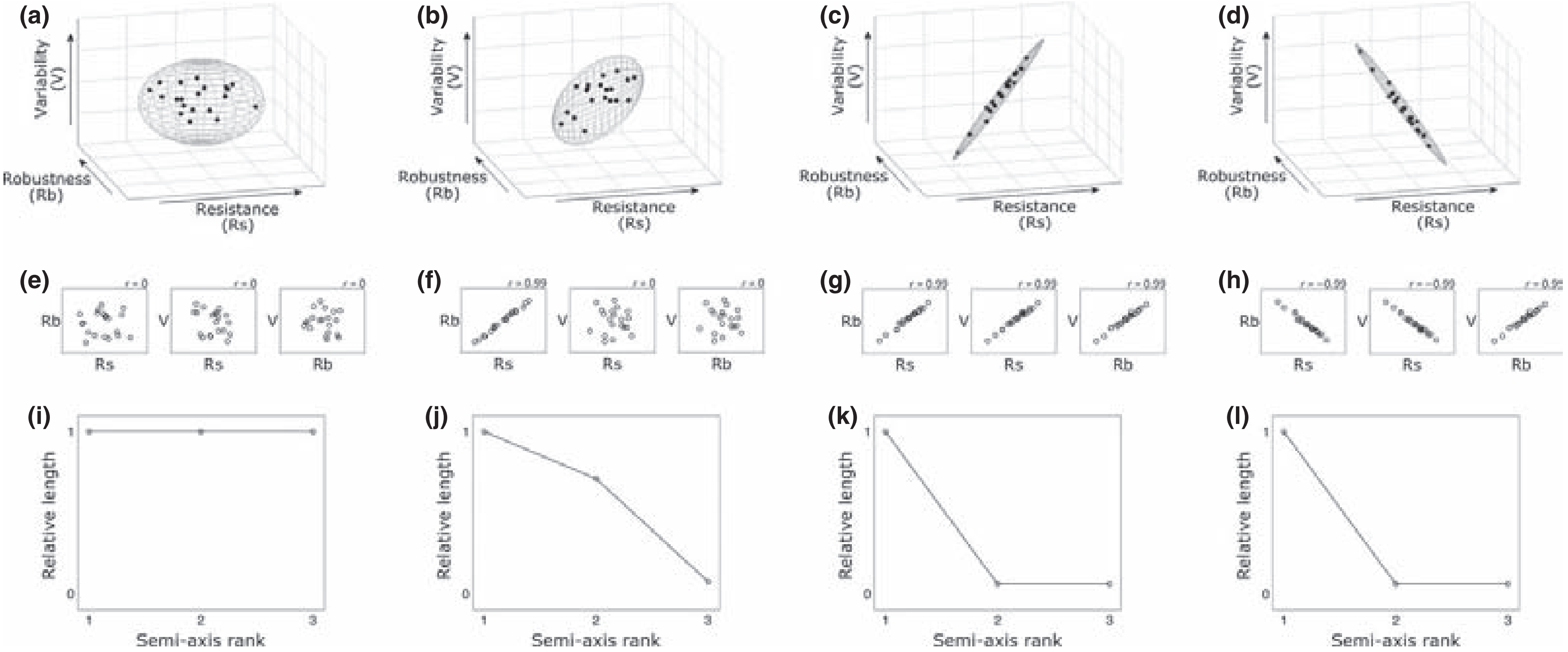
In this chapter, we develop the concept of ecological stability in a multidimensional framework and explore the two key questions about the interrelationships among different stability measures. As an example of how this framework can be applied, we conducted a manipulative field experiment on marine rocky shore communities comprising primary producers, primary consumers (prey) and predators. Six measures of stability were quantified (table 3.1), representative of a range of components of ecological stability. We hypothesised that ecological stability has relatively low effective dimensionality but that the loss of different species can trigger distinct shifts in the strength and nature of relationships among stability components and increase the effective dimensionality of stability. To maximise the ecological realism of our results, we conducted the experiment in a natural ecosystem containing established communities structured by a diverse range of both trophic and non-trophic interactions [63, 173].

3.2 Methods

Our experimental site was located on the mid to low shore at Rush (53 °31.4’ N, 6 °04.9’ W) on the east coast of Ireland on a moderately exposed flat rocky reef containing networks of patches of bare rock, mussels, barnacles and macroalgal stands. Each plot contained approximately 50% mussel cover prior to the random allocation of treatments (range 45-55%). There was no difference in macroalgal communities among treatments at the commencement of the experiment (`PERMANOVA`; Pseudo-$F_{9,30}$ = 0.81, P = 0.82).

We perturbed our experimental plots by simulating the loss of two predator species [whelk (*Nucella lapillus*) and crab (*Carcinus maenas*)] and two groups of their primary consumer prey [mussels (*Mytilus edulis*) and molluscan grazers, comprising principally *Patella vulgata*, *Littorina littorea* and *Gibbula umbilicalis*] over 14 months using wire mesh cages (figure 3.1a). Experimental manipulations mimicked as closely as possible natural patterns at the experimental site. The stainless steel mesh cages used to manipulate the presence of target consumers (0.9 mm wire diameter, 3.33 mm aperture, 61% open area) measured 35 x 35 cm and were 12 cm high, allowing for algal growth and recruitment. This cage design has been used extensively and successfully to manipulate consumer presence on rocky shores with no consequences for algal community structure [182, 183]. The cages allowed immigration and recruitment of primary producers and many epibenthic consumers, including primary consumers and small predators (e.g. amphipods, polychaetes and Nemertea). We thereby caused the local extinction of key components of a larger intertidal food web in an open experimental system without removing all consumers from a given trophic level. The fences were attached to the shore by drilling holes into the rock and securing them with stainless steel screws and washers. Roofs were also made

Box 1 The dimensionality of ecological stability



Four scenarios illustrating a spectrum of possible relationships among three different dimensions of stability; variability (V), resistance (Rs) and robustness (Rb) are used in this example, though in reality there will often be more than three components: (a, e, i) the three components of stability are independent, ecological stability is a relatively complex phenomenon with relatively high effective dimensionality; (b, f, j) two components of stability are strongly correlated and both independent of the third; (c, g, k) all measures of stability are strongly and positively correlated, ecological stability is a relatively simple phenomenon, with low effective dimensionality; (d, h, l) all measures of stability are strongly correlated, but some of those correlations are negative; ecological stability again has low effective dimensionality. The relationships among the three components of stability for the four scenarios are illustrated as ellipsoids in multidimensional stability space in (a-d) [(a) spherical, (b) 'frisbee'-shaped and (c, d) 'cigar'-shaped], which were constructed using the covariance matrix of stability measures (see *Methods*); as sets of pairwise scatterplots in (e-h), with associated Pearson correlation coefficients (r), and using the relative (to the dominant axis) lengths of ellipsoid semi-axes in (i-l). The relative length of any ellipsoid semi-axis is proportional to the amount of variation along that axis, meaning that the distribution of relative lengths among axes defines the dimensionality and shape of the ellipsoid. Similarly, the volume of the ellipsoid describes the total variation in stability, while changes in ellipsoid orientation indicate shifts in the relative magnitude and/or form of correlations among stability measures. The orientation of the ellipsoid in (c) is orthogonal to that in (d) (i.e. the angle between the dominant eigenvectors of each ellipsoid is 90 °).

from the stainless steel mesh and were fixed to the tops of the fences with cable ties. Cages and treatments were checked and maintained regularly (approximately every 2 weeks) and cages were scrubbed routinely with a wire brush to remove any algae.

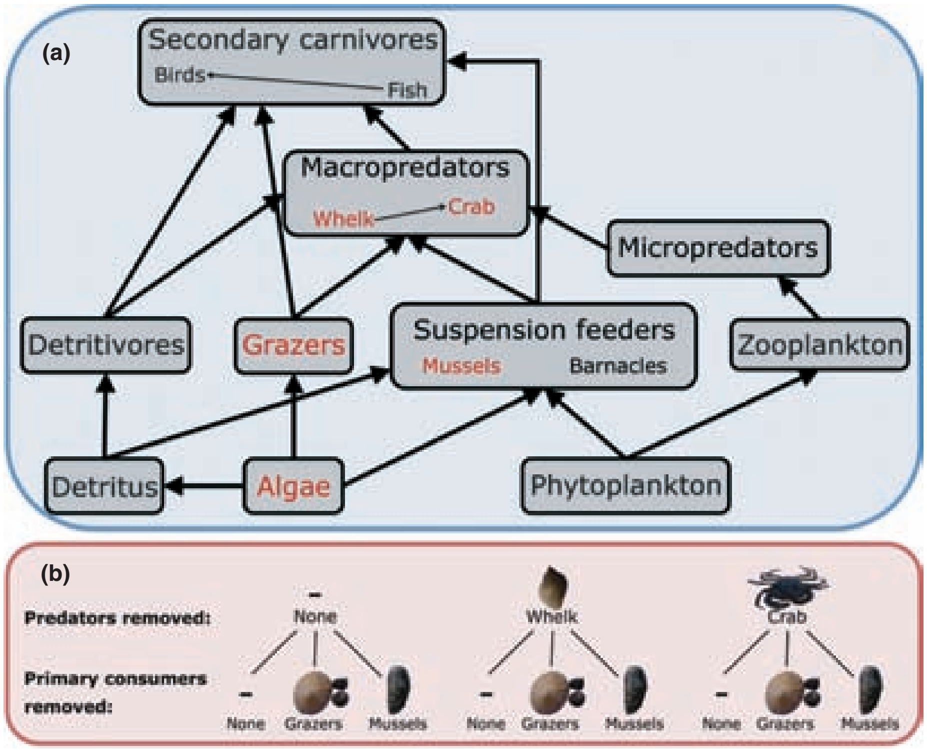


Figure 3.1: (a) Simplified trophic interaction network on moderately exposed rocky shores (adapted from [131]). Highlighted in red are consumers whose presence was manipulated (see Methods). We quantified the effects of these experimental species extinctions on multiple components of the stability of macroalgal communities (also highlighted in red). (b) Our experimental design comprised two fixed factors: 'predators removed' and 'primary consumers removed', each comprising three levels (predators removed: no removal, whelk removed and crab removed; primary consumers removed: no removal, grazers removed and mussels removed). Comparison of the resulting nine treatments enabled us to quantify the individual and combined effects of consumer species loss across multiple trophic levels on the stability of macroalgal communities.

Our experimental design comprised two crossed fixed factors, with three levels in both [loss of predators (no predators removed, whelk removed, crab removed) and loss of primary consumers (no primary consumers removed, grazers removed, mussels removed)], resulting in a total of nine caged treatments (figure 3.1b). Each of our experimental treatments was replicated four times. Mussels and molluscan grazers were removed manually from treatments to simulate loss of these species. Although mussels do not consume benthic macroalgae, they comprise important consumers of macroalgal propagules [228]. They also have strong non-trophic interactions with macroalgae arising primarily from competition for space on the shore [142, 181] and these interactions vary in the presence of grazers [55]. Predators were placed in the plots as required for the treatment at a density of one individual per plot. Crabs found on the shore and used in the experiment had a carapace width of 3-6 cm. This size range of crab feeds mainly on mussels and small grazers [218]. Although larger crabs have been found to feed on whelk (e.g. [103]), no predation by crabs upon whelk was observed during our experiment.

We quantified the extent of cover and composition of macroalgal communities on each plot with a 25 x 25 cm double-strung quadrat four, seven, ten and fourteen months after the commencement of the experiment. The quadrat was placed in the middle of each plot to avoid sampling edge effects and the cover and composition of algae estimated by identifying all species present under each of 64 intersections. Species of macroalgae present within the quadrat but not recorded under an intersection point were noted and assigned a value of 1% cover. Given that algal cover varied along vertical as well as horizontal axes, total algal cover within experimental plots frequently exceeded 100%.

Algal communities on rocky shores are highly dynamic and can change dramatically within a few months, particularly at the scale of individual plots, driven by dynamic interactions between environmental fluctuations and biological interactions (e.g. [95]). Consequently, by focusing our efforts on primary producers, we maximised the probability of detecting relatively rapid shifts in stability [31]. We quantified the following six measures of the stability of macroalgal communities, representing a range of components of ecological stability [202]: the temporal and spatial variability of total algal cover; the compositional turnover of algal communities over time (the reciprocal of persistence); the number of extinctions (structural robustness) and invasions (another measure of persistence) of algal taxa and the resistance of algal communities to perturbations. These components of stability and the methodologies used to quantify them are described in table 3.1.

Pairwise relationships among stability components were quantified using Pearson correlation coefficients. We used principal components analysis (PCA), based on standardised data (calculated by subtracting the means and then dividing by the standard deviations to remove differences in scales of measurement), to examine the effective dimensionality of stability. Unlike the other measures of stability, spatial variability was not associated with individual experimental plots and could not be incorporated in the PCA.

We used modified Mantel tests to compare the volume, orientation and shape of ellipsoids in multidimensional stability space (see Box 1). Ellipsoids were constructed from the matrix of pairwise covariances between components of stability. All measures of stability were standardised (as described above for PCA) to remove differences in scales of measurement prior to the construction of ellipsoids. As spatial variability was not associated with individual experimental plots and could not be used in the calculation of covariance matrices, ellipsoids were quantified in five rather than six dimensions. We generated null distributions of effect sizes using a series of permutation analyses, where we reassigned each observation to a treatment group randomly without replacement 10^4 times. We focused our analytical comparisons of ellipsoids on tests for effects of the loss of primary consumer species. This was done to maximise the number of samples used to construct the ellipsoids and because the loss of primary consumers affected every measure of stability in some way and was the only factor that had significant main effects in the absence of interactions.

Ellipsoid volume (V) was calculated for each treatment group in both the observed and permuted datasets using the formula:

$$V = \frac{\pi^{n/2}}{\Gamma\left(\frac{n}{2}+1\right)} \prod_{i=1}^{n} (\lambda_i^{0.5})$$

where λ_i is the *ith* eigenvalue of the covariance matrix for a given treatment and *n* is the dimensionality of the covariance matrix of standardised stability measures. We tested the significance of pairwise differences in observed volumes between treatments by comparison with the null distribution of differences from the permuted data. The orientations of the dominant eigenvector (v_1) for each treatment were compared in a similar pairwise manner. The smallest angle (ϑ) between the dominant eigenvectors ($v_{1,i}$ and $v_{1,j}$) of treatments *i* and *j* is a function of their dot product by the equation:

$$\vartheta = min([cos - 1(V_{1,i} \cdot V_{1,j})], [\pi/2 - cos - 1(V_{1,i} \cdot V_{1,j})])$$

The null distribution of angles between eigenvectors was created using the permuted null dataset and observed values compared against it to test for significance. As angles are inherently dyadic and positive, we used one-tailed tests to test for pairwise differences in orientation between treatments. Finally, we compared the shape of ellipsoids by using the distribution of the semi-axis lengths ($a_i = \lambda_i^{0.5}$). We standardised each set of ellipsoidal semi-axis lengths by dividing by their maximum. Pairwise comparisons of differences in relative lengths for semi-axes were then evaluated against the respective null distributions of differences.

We tested for effects of our experimental manipulations on individual components of stability using analysis of variance (`ANOVA`) after first ensuring homoscedasticity with Cochran's test. Each of the spatial variability, number of extinctions and detrended temporal variability of algal communities were square-root transformed to homogenise variances prior to analysis.

3.3 Results and discussion

When considering assemblages within plots as a set of local communities that vary in species composition and are exposed to the same relatively weak perturbations (i.e. natural fluctuations in environmental conditions), all pairwise correlations among the six components of stability were significant ($P < 0.05$) and frequently strong ($r > 0.7$ for seven of the 15 pairwise correlations; figure 3.1). Temporal and spatial variability, compositional turnover and the number of extinctions were all correlated positively with one another and negatively with the number of invasions and resistance. PCA (quantified here in five dimensions because spatial variability could not be associated with individual plots) revealed that over 64% of the variability among communities in multidimensional stability space could be accounted for in a single dimension, 80% in two dimensions, and 92% in three (table 3.1). Without correlations among stability components, we expect these figures to be, respectively, 20, 40 and 60%. The first principal component was related positively to compositional turnover and resistance (eigenvector loadings of 0.5 in both cases), whereas the second principal component was determined strongly by the number of invasions (-0.94). These results demonstrate that the effective dimensionality of stability can be comparatively low and collapsible to just two or perhaps three dimensions. Thus, ecological stability appears to be less complex, perhaps even considerably so, than it otherwise could be.

Analysis of the shape, volume, and orientation of stability ellipsoids (sensu Box 1) reveals that our experimental perturbations changed both the dimensionality and nature of ecological stability. The loss of primary consumer species altered ellipsoid shape, from a 'cigar'-shaped ellipsoid when no primary consumers were lost towards increasingly spheroidal ellipsoids in the absence of mussels and, in particular, grazers (figure 3.2a). In fact, the loss of grazer species increased the relative length of multiple ellipsoidal axes significantly (figure 3.2b), indicating that perturbations can decouple relationships among stability components (Box 1) and, thus, increase the effective dimensionality of stability.

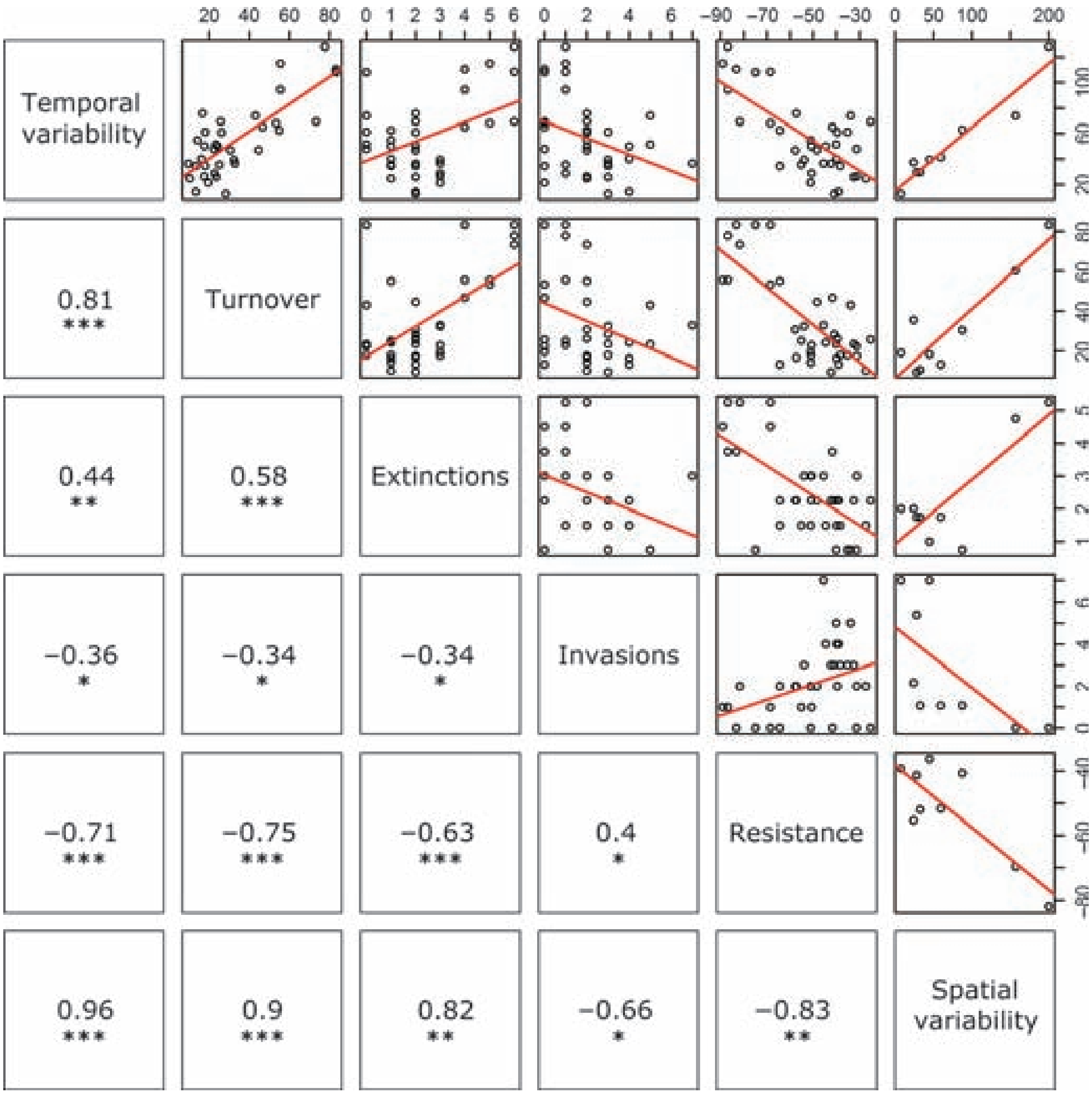


Figure 3.1: Pairwise relationships among multiple components of ecological stability. Scatterplots and associated Pearson correlation coefficients for the pairwise relationships between each of our measures of stability at the among-community ecological scale. As spatial variability was quantified as the variability among plots within each of our nine experimental treatments (see Methods) and could not therefore be associated with individual plots, we used the mean treatment value for each measure of stability in all pairwise correlations involving spatial variability. $*P < 0.05, **P < 0.01, ***P < 0.001$.

Although reductions in ellipsoid volume after the loss of primary consumers were not statistically significant (pairwise differences in ellipsoid volume for random permutations of the data and observed treatments: (i) grazers lost-no primary consumers lost: $P = 0.1$; (ii) mussels lost-no primary consumers lost: $P = 0.095$; grazers lost-mussels lost: $P = 0.95$), we found that the loss of either mussels or grazers, irrespective of the presence or absence of their predators, altered the orientation of ellipsoids significantly (figure 3.2c). So extreme were changes in the nature of interdependencies among components of stability that ellipsoid orientation after mussel loss was effectively orthogonal to that when no primary consumers were removed (figure

Principal component	Eigenvalue	% Variation	Cumulative % variation
1	3.21	64.2	64.2
2	0.774	15.5	79.7
3	0.593	11.9	91.5
4	0.254	5.1	96.6
5	0.169	3.4	100

Eigenvectors

Variable	PC1	PC2	PC3	PC4	PC5
Temporal variability	0.478	-0.211	-0.494	0.270	0.640
Compositional turnover	0.502	-0.261	-0.192	0.310	-0.739
Extinctions	0.417	-0.013	0.833	0.304	0.199
Invasions	-0.310	-0.936	0.147	-0.055	0.059
Resistance	0.500	-0.105	0.061	-0.857	0.001

Table 3.1: Results of principal components analysis (PCA) of multidimensional stability in our experimental plots. Spatial variability was omitted from this analysis as it could not be associated with individual plots.

3.2c), meaning that the dominant relationships among components of stability shifted to almost the theoretically maximal extent. These findings demonstrate that perturbations can modify the interrelationships among components of stability in many different ways, altering not only the strength of those relationships but also causing potentially dramatic shifts in their form.

In concurrence with these multivariate findings, we found that, while some components of stability responded similarly, others responded in different ways to different perturbations (i.e. the loss of different consumer species; figure 3.3). The loss of predator species in isolation, for example, altered four of our six measures of stability significantly; each of the temporal variability of total algal cover (`ANOVA`, $F_{4,27} = 4.53$, $P = 0.006$), the number of extinctions ($F_{4,27} = 3.81$, $P = 0.014$) and the compositional turnover ($F_{4,8} = 5.43$, $P = 0.021$) of algal taxa increased significantly following the loss of one or either predator species, while multivariate algal community structure also had significantly less resistance ($F_{4,27} = 4.1$, $P = 0.01$) to the loss of either predator species than to any other experimental perturbation (figure 3.3). These destabilising effects of predator species loss occurred when the primary consumer trophic level was intact and disappeared when either grazers or mussels were lost in tandem with either predator, resulting in significant interactions between predator species loss and the loss of their prey. In fact, the loss of mussels in combination with crabs even reduced the temporal variability of macroalgal cover significantly (figure 3.3). In contrast, two components of stability were affected solely by the loss of primary consumers irrespective of the presence or absence of their predators: the number of invasions of algal taxa increased significantly ($F_{2,27} = 8.05$, $P = 0.002$) following the removal of mussels, whereas the loss of either of the manipulated primary consumer groups reduced the spatial variability of total algal cover ($F_{2,27} = 8.47$, $P = 0.001$; figure 3.3).

Given that different scenarios of biodiversity loss altered different components of stability in disparate ways, our results demonstrate that perturbations can not only modify the shape and orientation of stability ellipsoids but they can also shift the location of communities in multidimensional stability space distinctively along different dimensions of stability. This multifaceted nature of stability cautions against focus on individual forms of stability in isolation,

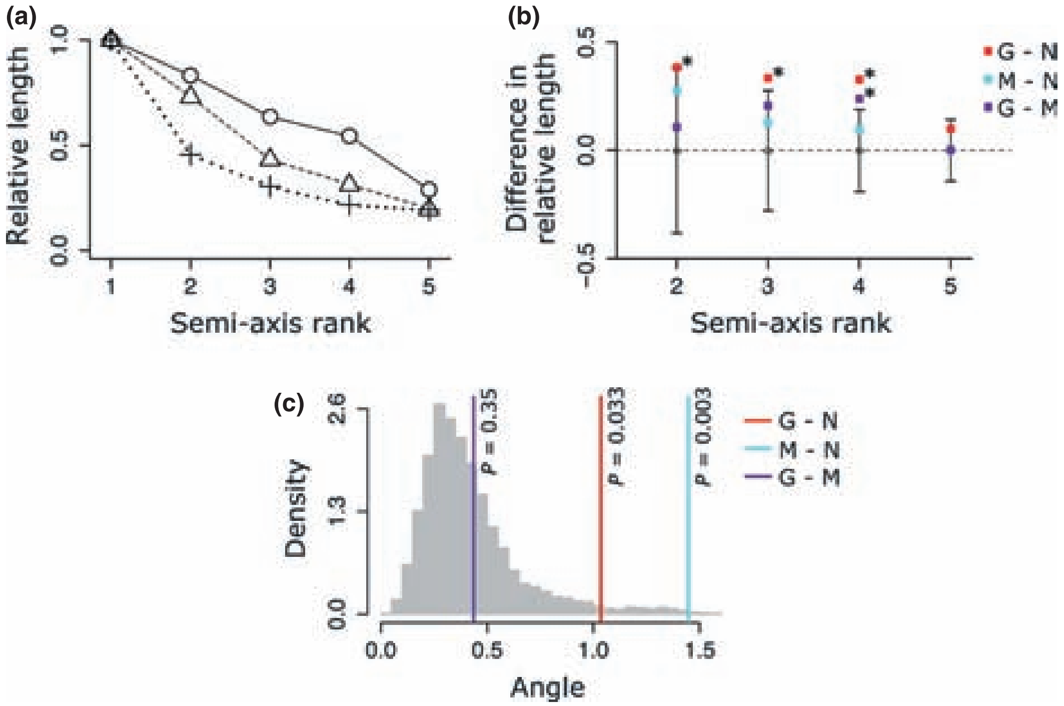


Figure 3.2: Effects of primary consumer species loss on the shape and orientation of ellipsoids in multidimensional stability space. (a) Relative lengths of ranked ellipsoidal semi-axes where no primary consumers were removed (+), after mussel loss ( ) and after grazer loss (○). (b) Pairwise differences in relative semi-axis lengths for random permutations of the data (95% CI shown here) and observed treatments [No primary consumers lost (N), Grazers lost (G), Mussels lost (M)]. Semi-axes with significantly ($P < 0.05$) greater relative lengths than the null distribution are highlighted with asterisks. (c) Pairwise differences in the angle (in radians) between dominant semi-axes (i.e. eigenvectors) for random permutations of the data (grey histogram) and observed treatments [No primary consumers lost (N), Grazers lost (G), Mussels lost (M)].

as this could considerably underestimate the potential of different perturbations to alter overall ecological stability.

We have shown that the dimensionality of ecological stability can be considerably lower than one would expect were the various components of stability unrelated. This implies that ecological stability may be a relatively simple concept, or at least not show as high dimensionality as there could be. It remains to be seen how the dimensionality of stability varies across different types of community to the one analysed here. In our experiment, changes in species composition caused changes in the dimensionality of stability and the interrelationships among its components, which suggest that the complexity and nature of stability may not be fixed across communities. In addition, the form of correlations among components of stability is also of great interest. In particular, negative correlations between different components of stability imply some mechanism akin to a trade-off between these components. Such trade-offs would have profound implications for ecosystem management, necessitating the prioritisation of some components of stability (e.g. enhancing agricultural yield reliability by minimising temporal variability in biomass) while accepting reductions in others (e.g. increasing susceptibility to invasion by exotic species). Although there is much to learn about this emerging field, we contend that a multidimensional stability framework gives us a richer understanding of how

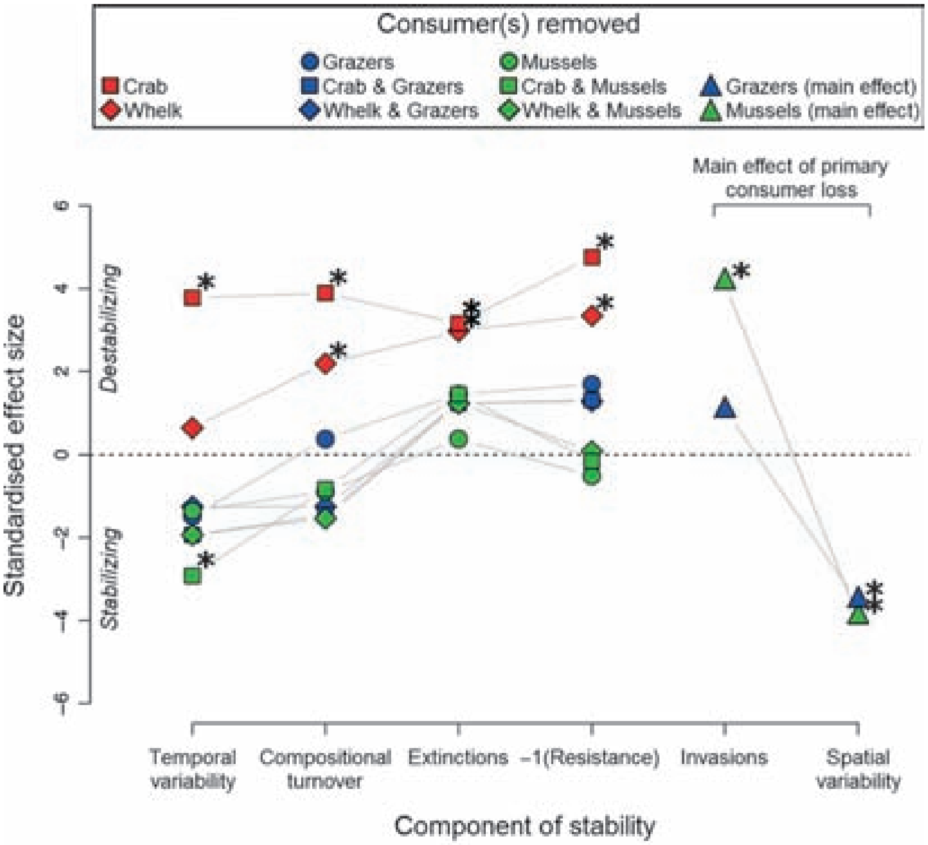


Figure 3.3: Effects of the loss of different consumer species on individual components of ecological stability. Standardised effect sizes based on the difference between experimental treatments and the corresponding treatment with no species removals. Treatments that differed significantly ($P < 0.05$) from the latter are highlighted with asterisks. The inverse of resistance is shown here so that all positive effect sizes correspond to reductions in stability. As the number of invasions and the spatial variability of algal cover were affected only by the loss of primary consumer species, effect sizes for these components of stability are shown only for the main effect of primary consumer loss.

communities respond to perturbations and is fundamental to support the optimal management of both biodiversity and ecosystem functioning.

Our study adds a new fundamental direction to recent research in developing a deeper and more comprehensive understanding of ecological stability (e.g. [152, 3]). Although we might expect most, if not all, measures of stability to be highly correlated in communities with different compositions, different perturbations are likely to alter and even decouple these strong dependencies in very different ways that are, consequently, difficult to predict. There is, therefore, much need for theoretical development and additional empirical studies both to elucidate mechanisms underpinning relationships among components of stability and to generalise our findings. Whether transient or permanent, changes in the interrelationships among different components of stability comprise one of the major consequences of biodiversity loss and global change.

Chapter 4

Network complexity and species traits mediate the effects of biological invasions on food webs

Miguel Lurgi, Núria Galiana, Bernat C. López, Lucas Joppa, José M. Montoya

In review in Ecology Letters

Abstract

Biological invasions are a major threat to natural communities worldwide. While several species traits have been identified as important determinants of invasion success, a systematic exploration of the effects of biological invasions on native communities, and the role of species and community features on community robustness in the face of invasion is lacking. We adopt a theoretical approximation considering food web structure and species population dynamics to study the effects of invasions on complex food webs . We find that less complex (i.e. less connected) and more internally-organised (e.g. more modular) food webs are more resistant to invasions. Simulated invasions promote profound changes in several food web properties. Additionally, species traits such as body size and diet breadth are strong determinants of invasion success across several trophic levels. Our work complements species-centred invasion studies by adding a more holistic and systematic perspective to the study of invasions on species interaction networks.

4.1 Introduction

Biological invasions are one of the main threats to biodiversity worldwide with far reaching consequences for ecological communities and local economies [263, 44]. Ever since the seminal work by Elton (1958) [76], ecologists have sought to understand biological invasions on natural communities.

Two main strains of research have derived from these efforts: (i) understanding the effects of invasions on native communities (e.g. [263, 235]), and (ii) identifying common features -from both native communities and invasive species- that allow predictions of invasion success (e.g. [124, 232]).

Invasions usually decrease native biodiversity and reduce population abundances [26, 118, 261], and affect ecosystem functioning [269, 235], although in some cases local increases in biodiversity have been observed [229, 269]. The impacts of invasive species on native communities are however, heterogeneous and not unidirectional [261], making general predictions of species response and effects too system-dependent and idiosyncratic. At present, we lack a more general and predictive framework for understanding the effects of species introductions in complex networks of interacting species.

Several traits have been identified as successful predictors of invasion success. These traits vary across the taxonomic group of the invader under consideration (e.g. [274, 124, 46, 213]). As a consequence, some researchers have claimed that there are no rules governing the invasion process with any real predictive value [34] because invasion success is strongly species or taxonomic group-dependant.

The characteristics of the invaded community also mediate invasion success. Experimental studies have shown the importance of the structure of multitrophic communities for the establishment of invaders: zooplankton diversity, for example, provides biotic resistance against invasion by algae [74]. However, the difficulties associated with collecting empirical data from large species interaction networks call for theoretical approximations to address this issue. Several authors have suggested comprehensive theoretical frameworks for the study of invasions in a community context [232, 256, 28], and to include biological invasions into even more general frameworks of community responses to climate change [86].

The role of food web structure in determining invasion success has long been recognised in the theoretical literature. For example, early theoretical competitive community assembly experiments, with simple Lotka-Volterra dynamics, showed that more connected [203] and strongly interacting [45] communities were more resistant to invasion. These studies however, used small and randomly assembled communities, and only addressed which community features made them more robust against invasion. Theoretical explorations within larger communities displaying more realistic food web structures are needed to determine both the role of food web complexity and species traits on invasion success.

Recently, Romanuk *et al.* [2009] [223] explored a number of food web and invader properties that predisposed species to successfully invade model communities. Using more realistic food web configurations and population dynamics determined by a bio-energetic model, they found that more complex communities were more robust to invasions, with complexity measured as network connectance (i.e. the fraction of realised links in the web). The trophic position and generality (i.e. number of prey species) of the invader were the best predictors of success.

Here we integrate food web structure and nonlinear population dynamics in large, complex model communities. Our study represents a step forward in at least three main respects: (i) identify key features of food webs (in addition to species richness and connectance) that make them more robust to invasions, (ii) investigate the effects of invasion on several community properties, and (iii) explore traits that can determine species invasion success.

Our aim is to answer the following questions: What are the effects of biological invasions on the structure and dynamics of complex food webs? What species traits do affect invasion success in food webs? What food web properties determine its vulnerability to biological invasions? In doing so, we test the following related hypotheses: (a) successful invasions alter food web structure and dynamics and make native communities more susceptible to further perturbations, (b) species with larger body sizes, more abundant, and more able to capture prey will be more successful invaders, (c) generalist consumers and prey attacked by less predators are likewise more capable of invading communities, and (d) more complex communities are more robust to invasions.

4.2 Material and methods

4.2.1 Food web generation

Food web structure of native communities was obtained using the niche model [272]. This model generates food webs by simply using the number of species (S) and connectance ($C = L/S^2$) of the network as input parameters. It is based on an algorithm that arranges species in a one-dimensional ‘niche’ and assigns predator and prey links to each species in the network in a hierarchical way.

We performed in silico invasion experiments on food webs containing 60 species (S = 60) and 3 different values of connectance (C = 0.05, 0.1, 0.15) that fall within the range observed in empirical food webs [272]. This allowed us to have relatively species-rich communities with different levels of complexity -defined here by C. Previous studies looking at several aspects of community dynamics and stability using a similar bioenergetic model, have considered smaller communities, up to 40 species [38, 23] or 30 species in the case of Romanuk *et al.* [223].

4.2.2 Non-linear model for population dynamics

For simulating species population dynamics we used an allometric version of the bio-energetic model originally proposed by Yodzis and Innes [283], which was updated with new allometric coefficients [41] and extended to multispecies systems by Williams and Martinez in [273]. In this model, the change in species biomass through time is given by:

$$\dot{B}_i = r_i G_i B_i - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{4.1}$$

$$\dot{B}_i = -x_i B_i + \sum_k x_i y_i B_i F_{ik} - \sum_j \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{4.2}$$

Equations 4.1 and 4.2 give the rate of change in biomass through time for producers and consumers in the food web, respectively. B_i and B_j denote the biomass density of populations i and j, r_i is the mass-specific intrinsic growth rate of producer species i, and G_i is the logistic growth function. $x_{i,j}$ denotes the mass-specific metabolic rates of species i and j, $y_{i,j}$ the consumers maximum consumption rate relative to its metabolic rate, and e_{ji} is the assimilation efficiency of consumer j when consuming prey i. The subscript k denotes the resources of i, and the subscript j its consumers. F_{ji} corresponds to the functional response (detailed in equation 4.4).

The term for the logistic-growth is given by:

$$G_i = \left(1 - \frac{B_i}{K_i}\right) \tag{4.3}$$

which assumes that the growth of each basal species i is dependent on its carrying capacity K_i. Thus, G_i describes i's population biomass deviation from K_i.

In equations 4.1 and 4.2, $F_j i$ corresponds to the functional response (i.e. the resource density-dependant feeding rate of consumer j on a resource i influenced by all the other resources k of j). F_{ij} is defined as:

$$F_{ji} = \frac{\omega_{ji} B_i^h}{B_0^h + cB_j + \omega_{ji} B_i^h + \quad {}_{k}\,\omega_{jk} B_k^h} \tag{4.4}$$

where ω_{ji} is a dimensionless positive weight factor sometimes used to simulate prey preference, but that here is set to 0.5 for all interactions in order to ensure that predators do not exhaust their resources quickly without including prey preferences (see [123] for details), B_0 is the half-saturation density, and c and h correspond to predator interference and Hill exponent terms, respectively. The Hill exponent determines the shape of the functional response: a large Hill exponent renders the curve more sigmoidal, which is interpreted as a refugee effect for the prey at low densities.

Biological rates of production, metabolism and maximum consumption are scaled allometrically following [23]. We assume biological rates of production (R), metabolism (X) and maximum consumption (Y) scale as a negative-quarter power law relationship with species' body mass [41] as:

$$R_P = \alpha_r M_P^{-0.25} \tag{4.5}$$

$$X_{C,P} = \alpha_x M_{C,P}^{-0.25} \tag{4.6}$$

$$Y_C = \alpha_y M_{C,P}^{-0.25} \tag{4.7}$$

where C and P correspond to consumer and producer parameters, respectively; α_r, α_x, and α_y are allometric constants. In the model, the reproduction rate is normalised by the mass-specific intrinsic growth rate of the smallest basal species, j (R_j). This defines the time scale of the system.

$$r_j = \frac{R_j}{R_j} = 1 \tag{4.8}$$

$$r_i = \frac{R_i}{R_j} = \left(\frac{M_i}{M_j}\right)^{-0.25} \tag{4.9}$$

However, since the body size of all of the basal species in the model is constant and equal to 1, the reproduction rate for each one of them is given by equation (4.8), and is thus equal to 1 for all producers.

Similarly, the mass-specific metabolic rates (Eq. 4.6) are normalised by the production and hence, the time scale (Eq. 4.5):

$$x_i = \frac{X_{C,P}}{R_P} = \frac{\alpha_x}{\alpha_r}\left(\frac{M_{C,P}}{M_P}\right)^{-0.25} \tag{4.10}$$

Finally, the maximum consumption (Eq. 4.7) is normalised by the metabolic rates (Eq. 4.6), which after algebraic manipulation yields:

$$y_i = \frac{Y_C}{X_P} = \frac{\alpha_y}{\alpha_x} \tag{4.11}$$

thus, the maximum consumption rate remains constant for all species in the food web.

Inserting Eqs. (4.9)-(4.11) into Eqs. (4.1) and (4.2) yields a population dynamic model with parameters that are allometrically scaled.

In order to keep the energy content in the food web constant to compare different simulated webs, a system-wide carrying capacity ($K_{sys} = 5$) was used. Each primary producers' share from this K_{sys} (K_i in equation (4.3)) is calculated dividing it by the number of basal species in the food web.

Low values of K_{sys} have been found to provoke starvation of high trophic level consumers, whereas high values of that parameter usually trigger extinctions due to dynamic instabilities [43]. A value of 5 for K_{sys} is normally chosen for this type of experiments because is in the middle of these extremes and is still capable of allowing for a variety of cases to explore (see [23]).

As in previous theoretical works (e.g. [23], and references therein) we used parameter values that are within the range of values generally found in natural communities. For example, we used assimilation efficiencies of $e_{ji} = 0.85$ and $e_{ji} = 0.45$ for carnivore and herbivore links respectively while the maximum consumption rate of consumers was kept constant at $y = 8$, as well as the predator interference term, which was set to $c = 0.1$. The normalised metabolic rate (α_x/α_r) was set to 0.314 as in [38]. The hill exponent was set to $h = 1.5$, and the initial biomasses of species were randomly chosen from a uniform distribution between 0.1 and 1.

The body masses of the species increase with trophic position modified by a factor of 10^2. This way of calculating body mass allows for intra-trophic level variation while preserving the increase in mass with trophic level [220]. Even though trophic level and body mass are highly correlated, they can influence species' extinction risk independently.

4.2.3 Food web properties and community stability

Several food web properties were measured before and after invasion (figure 4.1). These included coarse-grained properties: number of species (S), connectance ($C = L/S^2$), and links per species (L/S), and fine-grained properties, including mean food chain length (MFCL), number of food chains (ChnNo), standard deviation of the generality (GenSD) and vulnerability (VulSD), fraction of producer (%B), intermediate (%I), and top predator (%T) species, and modularity (the degree to which the food web is modular, calculated using the netcarto algorithm [90]). A food chain is any directed path from a basal resource to any consumer in the food web. GenSD and VulSD quantify the variability in the standardised number of prey (G_i) and predators (V_i) of the species in the network respectively:

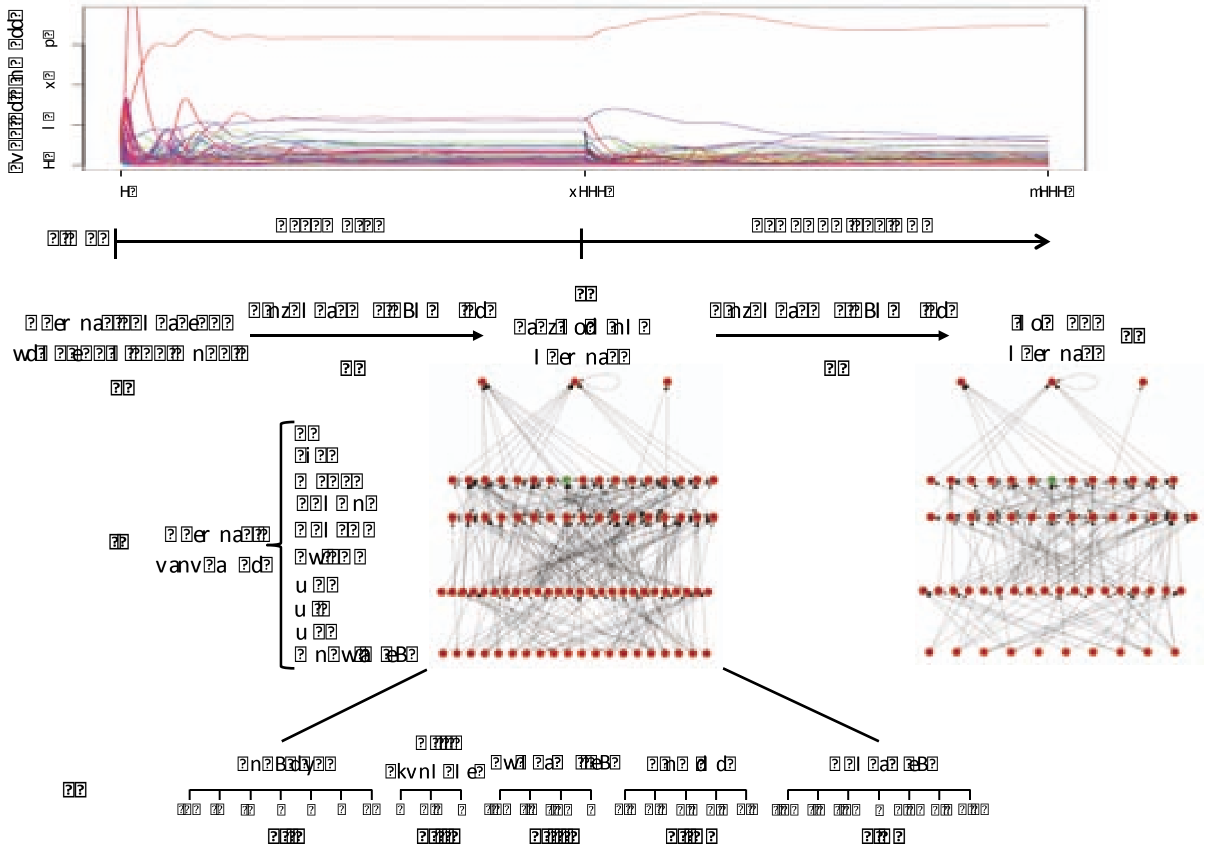


Figure 4.1: Conceptual diagram of the in silico experiments performed. (a) The initial food web structure of the community is generated using the niche model. (b) Community dynamics through a transient period (from iteration 0 to 2,000) are simulated using the bio-energetic model (see text). Communities that are stable at timestep 2,000 are subject to invasion (c). After invasion, the community evolves further 2,000 timesteps (to 4,000) (d) until it reaches a new state (e). Before introducing the invasive species a series of network properties are measured (f). These properties are again measured in (e) for comparison against their original values in (c) (before invasion). This process is repeated with several values for 5 different species traits (g.I-V) in order to test for the influence of variability within these traits on invasion success (see description of these experiments in the text, including the meaning of each trait value).

$$G_i = \frac{1}{L\ \ S}\sum_{j=1}^{S} a_{ji} \qquad V_i = \frac{1}{L\ \ S}\sum_{j=1}^{S} a_{ij}$$

where a_{ij} is equal to 1 whenever there exists a link between prey i and predator j.

Community dynamics were iterated for a period of 2,000 time steps before introducing the invasive species (figure 4.1). This was enough to reach stable dynamics in most of our simulations. A species was considered extinct if its biomass fell below 10^{-9}, since biomasses below this value stop having any observable effect on community dynamics.

We also measured two types of stability: (i) total community biomass stability and (ii) average coefficient of variation (CV) of species biomass. Total community biomass was measured as the sum of the biomasses of all species in the community at any given moment. We assumed a community was stable in terms of total biomass (i.e. it achieved 'total biomass stability') if this sum varies less than 10% over a period of 200 time steps. Species biomass CV was measured for each species over 200 time steps. Then we calculated the average CV (a proxy of total variation), and if this value was less than 0.1 across the period selected, we considered that the community achieved 'species biomass CV' stability. The 10% thresholds in maximum variability for determining whether a community is stable according to our stability metrics were arbitrarily chosen as a way of quantifying the maximum amount of change allowed before becoming unstable.

4.2.4 In-silico invasion experiments

We ran the niche model for the number of species in the native community plus one (i.e. S = 60 + 1). The invasive species was then selected randomly from the pool of species yielded by the niche model and removed from it, together with its interactions. In this way the original community was formed, along with the invasive species that was going to be introduced into that same community later. By generating the invasive species and its interactions following the same heuristic implemented by the niche model, we ensure an empty niche space that the invader is best placed to occupy.

Simulated communities were selected based on whether they met the stability criteria abovementioned and the number of species coexisting after this initial period. Communities with less than 80% of the initial number of species (i.e. 48) or that were not stable in terms of total community biomass after reaching time step 2,000 (figure 4.1), were not considered in the analyses. For the remaining communities we measured the food web properties described above, and then performed the introduction of the invasive species. We simulated 2,000 additional time steps (for a total of 4,000), and computed food web properties again (figure 4.1). Invasion success was measured as a categorical value, which could take one of two possible values (successful or unsuccessful), depending on whether the invasive species got extinct (its biomass dropped below 10^{-9}) before reaching the end of the simulation (iteration 4,000).

This procedure was repeated 300 times for each of the values of connectance considered (0.05, 0.1, 0.15) giving a total of 900 distinct model communities.

In addition to the 'standard' invasion experiment -i.e. with the default values for all of the species traits (values in bold under each experiment g.I-V in figure 4.1) - we performed several additional invasion experiments in order to: (i) test for the effects of particular species traits on invasive success, and (ii) explore whether trait variation had differential effects on the original food web. Simulations were thus replicated on each of our selected communities by varying the following traits (figure 4.1), which allowed us to test our hypotheses:

1. Body size: where the invasive could be either 2, 5, or 10 times bigger or smaller than in the standard experiment.

2. Ability to capture prey: where the invasive could take two distinct values for the Hill exponent, 1 and 2; simulating Holling type II and type III functional responses for the invasive consumer respectively.

3. Generality: where the invasive species could have 25%, 50% or 75% of its incoming links (as defined by the niche model) either removed or added; effectively diminishing or augmenting its prey number respectively. In the case of links removed, these were randomly chosen from the available prey for that species. In the case of added links, these were randomly selected from the pool of species that were prey of consumers from the same trophic level of the invasive.

These 3 sets of experiments allowed us to test specifically the mechanism of the ability to capture prey as a determinant of invasion success.

4. Vulnerability: where the invasive species could be 25%, 50% or 75% less vulnerable (i.e. have that fraction of reduced predation) than originally defined by the niche model. Predatory links removed were chosen randomly amongst the outgoing links of the invasive species.

   This set of experiments allowed us to test the mechanism of predator release for invasion success.

5. Abundance: where the initial biomass of the invasive species took values of either 0.1, 0.3, 0.4, or 0.5 (default value in standard experiments was 0.2).

   Lastly, propagule pressure, another mechanism proposed as important for invasion success, was tested through this final set of experiments.

The configurations described above yield a total of 22 distinct invasion experiments for each generated community (22 x 900 = 19,800 simulations in total).

The model, as well as the statistical analyses, was implemented using the R statistical package [214].

4.3 Results

4.3.1 Is food web complexity and structure a good predictor of invasion success?

More complex networks were more vulnerable to invasion. Higher connectivity (both in terms of C and L/S), and larger MFCL and ChnNo were significantly and positively associated with susceptibility to invasion (figure 4.1, table 4.A.1 in appendix 4.A). Similarly, networks with a lower standard deviation of the generality (GenSD), a smaller fraction of basal (%B) and top predator (%T) species, and lower modularity were more prompt to invasion (figure 4.1, table 4.A.1).

Both results combined suggest that even though more complex networks were more susceptible to invasions, a higher level of internal organisation of the food web (i.e. how species and links are distributed within the network) increased community robustness to invasions.

4.3.2 Do invasions make food webs less complex?

The main effect of invasions in our simulated communities was species loss, with communities losing on average 8 (s.d. = 6) species. Basal species were predominantly loss, decreasing their fraction in the post-invasion network, which in turn increased the fraction of top predators and intermediate species.

In general, food web complexity was reduced. While invasions increased connectance, other aspects of complexity were significantly reduced, with networks becoming less modular, and having less food chains (figure 4.2 and table 4.A.2 in appendix 4.A). Similarly, the standard deviation of generalism decreased following invasions.

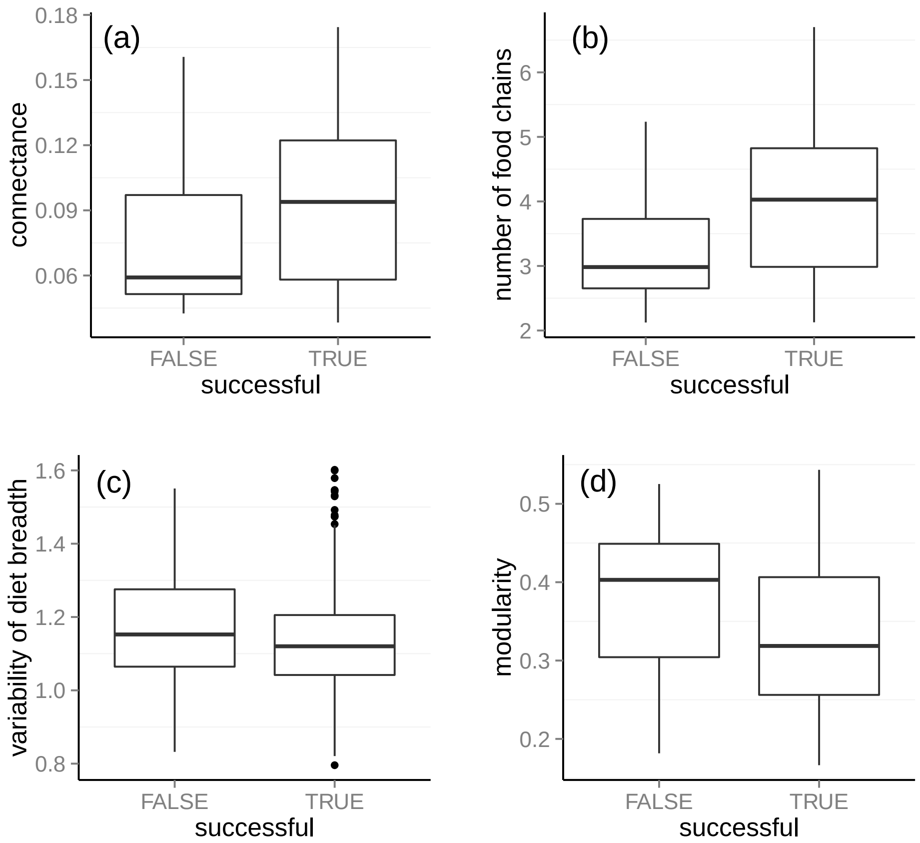


Figure 4.1: Relationship between food web properties and invasion success. In each panel, box plots correspond to the median value and the first (bottom of the box) and third (top of the box) quartiles of the distribution of each network property: (a) connectance ($C = L/S^2$), (b) Number of food chains (log(ChnNo)), (c) Standard deviation of generality (GenSD),and (d) modularity. In each panel, values of each property in communities with successful (True) and unsuccessful (False) invasions are compared.

This suggests that communities were losing resource input channels, with species composition getting biased towards higher trophic levels, and with consumers becoming more homogeneous in the number of different prey they attack (table 4.A.2).

When invasion attempts failed some of these food properties also changed. However, the effects caused by successfully established invaders were consistently stronger that those of unsuccessful invaders (data not shown).

4.3.3 Do invader traits affect their invasion success?

Are bigger species better able to invade communities?

Larger sizes of a given species were more successful invading a native community than smaller sizes (figure 4.3a, table 4.1), everything else being equal. The effects of body size on invasion success varied among communities with different connectance values. We found that it was more important to be bigger when invading less connected communities (figure 4.3a, table 4.A.3). This agrees with our finding that food webs with lower connectance were generally harder to invade (figure 4.1a). For a given species, being large is always beneficial for their

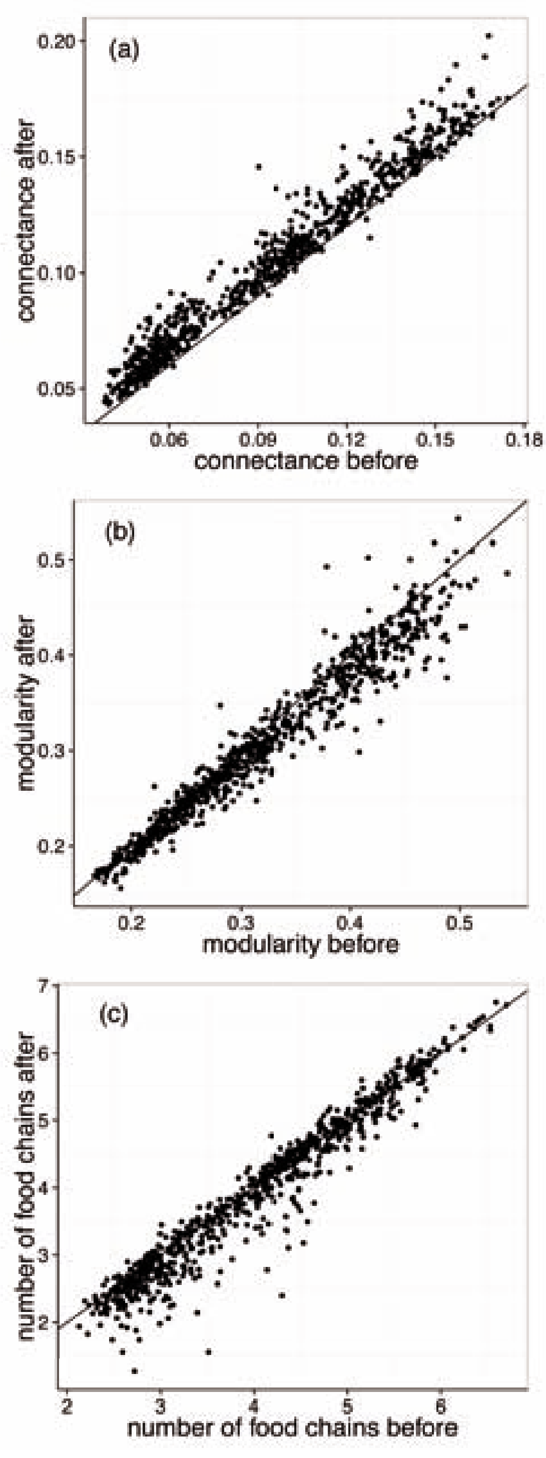


Figure 4.2: Effects of successful invasions on food web properties: (a) Connectance ($C = L \ S2$), (b) Modularity, and (c) Number of food chains (log(ChnNo)). Each dot corresponds to the same community before and after the invasion. 1:1 line corresponds to absence of change after the invasion. KS-tests performed to test for differences in the distributions before vs. after: C -$D = 0\ 1512$ $p < 0\ 001$-, modularity -$D = 0\ 0863$ $p = 0\ 002$-, and log(ChnNo) -$D = 0\ 0856$ $p = 0\ 002$- (see table 4.A.2 [in appendix 4.A] for results of KS-tests on other food web properties).

establishment success until some point, after which, no matter how large the species is, its likelihood of being successful does not increase. This point is reached when the invasive species is 5 times larger than its default body size values in the original model (figure 4.3a). The same phenomenon occurs for the 3 different values of connectance used.

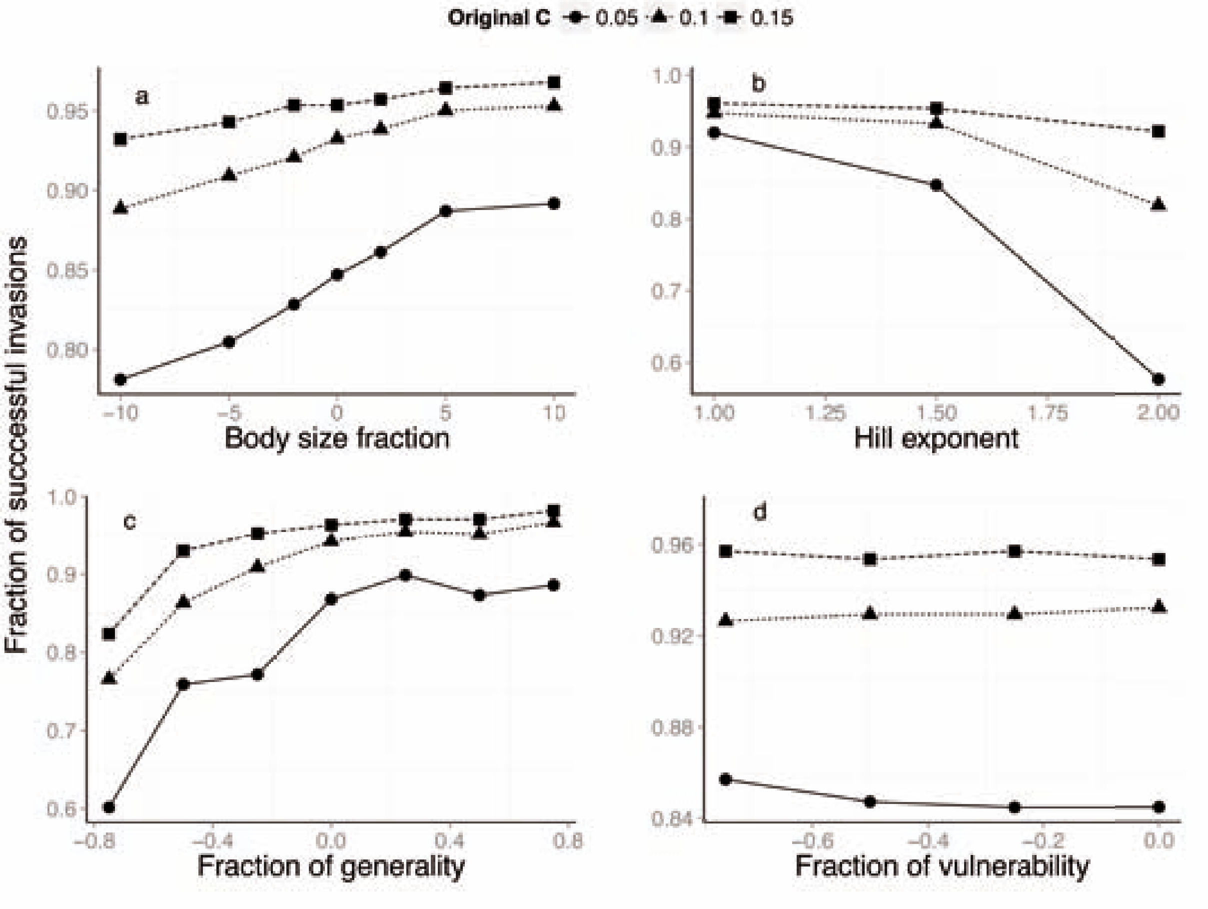


Figure 4.3: Effects of invader species traits on invasion success measured as the fraction of successful invasions for a given trait value. (a) body size: values represent species 10 (-10 and 10), 5 (-5 and 5), and 2 (-2 and 2) times smaller (−) or bigger (+) than the reference value for that species according to the bio-energetic model. (b) ability of the invasive species to capture prey (Hill exponent). (c) fraction of generality: fractions represent invasive species with 25% (-.25 and .25), 50% (-.5 and .5) and 75% (-.75 and .75) less (−) or more (+) prey than the species reference value. (d) fraction of vulnerability: values represent invasive species with 25% (-.25), 50% (-.5) and 75% (-.75) less predators than the reference. Circles, triangles, and squares correspond to the values of the fraction of invasion success for networks with connectance values of 0.05, 0.1 and 0.15, respectively.

Are species more efficient at capturing prey more successful invaders?

As expected, our results suggest that more efficient species capturing prey makes them more successful invaders. As for the effects of body size, it is more important to be more efficient in communities with lower values of connectance, which, as shown before, are harder to invade (figure 4.3b and table 4.A.4). In this case, however, the difference between the two extremes (i.e. functional response type II vs. functional response type III) is more pronounced than for the body size-connectance relationship, with differences up to 40% in the fraction of successful

Trait name	Trait value	Coefficient	z	*p-value*
Body size	-10	-0.46285	-3.330	< 0.001
	-5	-0.29189	-2.048	0.041
	-2	-0.12847	-0.877	0.3804
	2	0.10537	0.688	0.4914
	5	0.33213	2.064	0.039
	10	0.39218	2.403	0.016
Hill exponent	1	0.5261	3.109	0.002
	2	-1.2171	-9.344	< 0.001
Biomass	.1	-5.992e-15	0	1
	.3	1.130e-02	0.075	0.9401
	.4	1.130e-02	0.075	0.9401
	.5	1.130e-02	0.075	0.9401
Generality	-.75	-1.5640	-11.303	< 0.001
	-.5	-0.7896	-5.372	< 0.001
	-.25	-0.5716	-3.787	< 0.001
	.25	0.2767	1.570	0.1163
	.5	0.1003	0.592	0.5538
	.75	0.3117	1.755	0.0793
Vulnerability	-.75	4.670e-02	0.306	0.7599
	-.5	1.410e-14	0	1
	-.25	3.467e-14	0	1

Table 4.1: Effects of variation on invader species traits on invasion success. GLMs results presented correspond to the difference between the trait values on the table and the default value for each trait respectively (see text). Food web connectance was included into the GLM as a fixed factor. Values for each trait are defined in the caption of figure 4.3 and methods. Results for trait values that were not significant are not shown. The sign of the coefficient value represents the directionality of the relationship between that trait and the fraction of invasion success. Degrees of freedom for the models measuring the effect of body size = 7321, hill exponent = 3137, biomass = 5229, generality = 6964, and vulnerability = 4103.

invasions for less connected food webs (figure 4.3b). Differences between displaying the default functional response (i.e. Hill exponent = 1.5) and having a Holling type III functional response made invasive species significantly more successful (table 4.1). However, differences between the type II functional response and the default one, although still significant, were not as marked (table 4.1).

Is species biomass an important determinant of invasion success?

The biomass of the invasive species at the time of introduction did not affect its invasion success. For all the values tested in our trials the percentage of successful events relative to the total number of attempts remained constant (table 4.1).

Are more generalist species more successful invaders?

We found that, for species with the same niche value (as defined in the niche model), consumers attacking a smaller number of different prey items decreased their invasion success (figure 4.3c).

On the other hand, more generalist consumers were better at invading communities only until a given threshold, beyond which increasing the number of different prey species consumed did not affect its probability of invading successfully. The fraction of successful invasions reached a plateau and then remained relatively constant at values of .25 of the fraction of generality, i.e. having 25% more prey items had the same effect on invasion success than having 75% more (figure 4.3c and table4.1). In agreement with our previous results, it was more important to be more generalist in food webs with lower connectance values that are harder to invade. For example, for an invasive species that is 75% less generalist than expected by its niche value, the difference between successful and unsuccessful invasion attempts can go up to more than 20% between food webs with $C = 0.05$ against networks with $C = 0.15$ (figure 4.3c and table 4.A.5).

Is vulnerability a good predictor of invasion success?

Changes in the number of predators attacking the invasive species did not affect its probability of success (figure 4.3d). Even for large fractions of removed predatory links (e.g. -.75), the only noticeable increase in invasion success was observed for poorly-connected webs, with the fraction of successful invasions increasing by only 1% in comparison to the case in which the invader kept all of the perdators given by its niche position (table 4.1). Again, less connected webs were harder to invade, but predator release was not a strong determinant of invasion success.

4.3.4 Community stability

We found that network connectance determined which of the 2 stability measures (i.e. community biomass or species biomass CV stability) was achieved earlier after the invasion. In poorly connected food webs ($C = 0.05$), 41% of the times total community biomass stability was achieved earlier than species biomass CV stability, while only in 25% it was the other way around. In contrast, highly connected food webs ($C = 0.15$), after the invasion, tend to recover faster species CV (63% of the times) than total (18% of the times) biomass stability. Food webs with intermediate connectance ($C = 0.10$) behave like highly connected ones, although differences in achieving earlier each type of stability were less marked (figure 4.4).

As shown before, less connected communities were more robust to invasions. This suggests that achieving total biomass stability faster than mean species' populations CV stability might be a mechanism behind the robustness to biological invasions. Communities that maintain a relatively constant total biomass in spite of fluctuations at the species' population level may be more resistant to species invasions disrupting population dynamics.

4.4 Discussion

The link between community complexity and response to disturbances (i.e. stability and robustness) has been the subject of a long, heated, and far from finished debate in ecology [150, 151]. In the face of current global change, this research area has been reinvigorated. Here we have shown how food web structure and complexity mediates the vulnerability of communities to biological invasions.

We found that more connected food webs are more vulnerable to invasions. This contrasts with previous theoretical results by Romanuk *et al.* [223], because they found that more con-

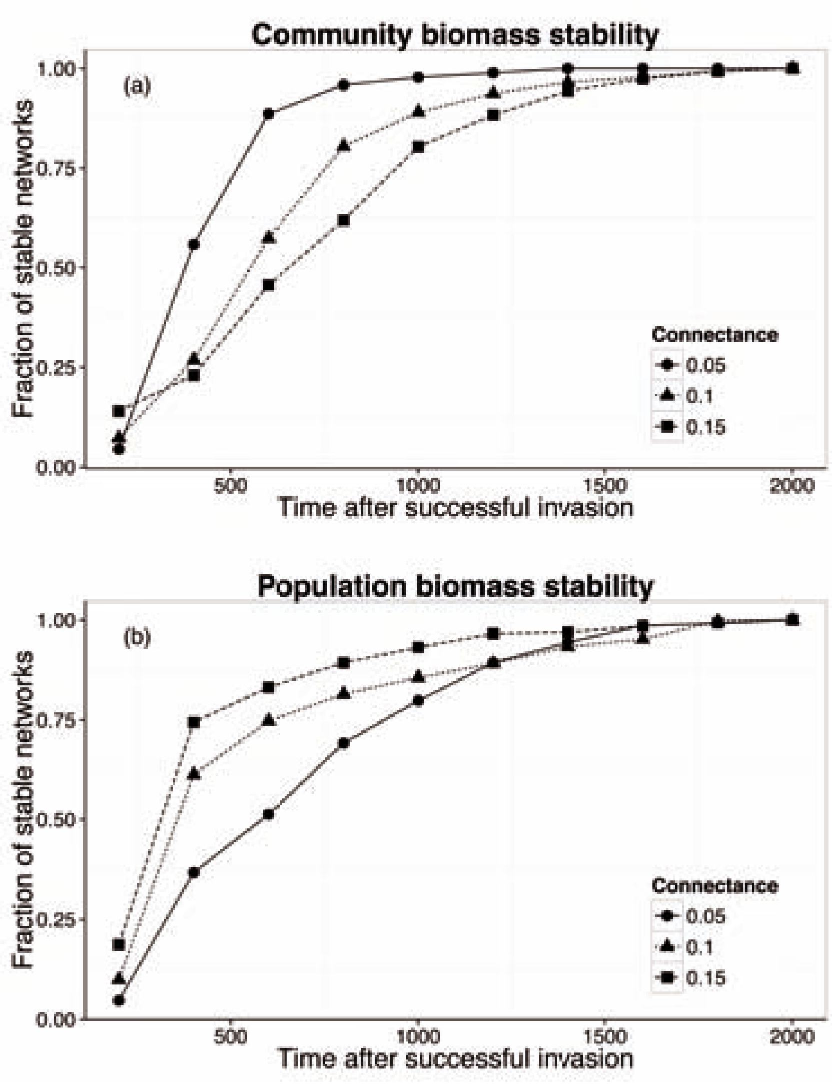


Figure 4.4: Food web stability analysis for communities with successful invasions. Cumulative fraction of stable networks over the time elapsed since the invasion is represented in terms of (a) total community biomass, and (b) mean species biomass CV, over the time elapsed since the invasion. Circles, triangles and squares represent the fraction of communities achieving stability at that time step for communities with connectance values of 0.05, 0.1 and 0.15 respectively.

nected food webs were more robust to invasions. These opposite results may arise from the relationship between species richness and connectance in both studies. Romanuk *et al.* used less speciose food webs than the ones used here (15 species on average in comparison to the 60 species used in the present study), but more importantly, they a priori assumed that more connected food webs were systematically less diverse. Theoretical and empirical studies generally show that higher levels of diversity confer resistance to invasions (e.g. [45, 203, 119]), and thus the effects of richness and connectance can be confounded. In this work we isolated the effect of connectance on invasion success by keeping diversity constant and relatively large. Once assessed independently and in relatively large food webs, higher levels of connectance likely increase vulnerability to invasions.

We found that not only complexity, but also the internal organisation of links within the food web is an important factor affecting the vulnerability of communities to invasions. Food webs containing consumers with very diverse diet breadths (from very specialised to generalists) were more robust to invasions. More heterogeneous communities in terms of diet breadth limit the availability of niches, which might prompt invasive species to face more competition when trying to establish in a community. This might seem contradictory with our finding that connectance increases the chances of successful invasions. Actually, one might be a consequence of the other. Communities with higher connectance necessarily bias the diet breadth continuum towards more generalist consumers. This in turn allows for niches that can be occupied by more specialised consumers to be readily available.

Another aspect of food web structure that has been linked to community stability and robustness is modularity. Thébault and Fontaine [249] found that food webs that are organised into compartments and that possess weakly connected architectures are more stable. In addition, a more modular architecture prevents the propagation of perturbations affecting population abundances across the whole network [164, 243]. Our results extend these previous findings to the context of biological invasions through the observed positive relationship between modularity and robustness to invasion.

In our model communities, those that were less connected and more modular were the most robust against invasions. Coincidentally, Thébault and Fontaine [249] found that precisely these are the features that confer stability to food webs. Stability thus, given by high modularity and low connectance, might be a likely mechanism behind robustness to invasion in complex communities.

A paradoxical relationship between complexity and stability after invasions is observed in our model communities. After an invasion, less connected food webs showed a higher stability in terms of total community biomass but lower stability in terms of variation on individual species biomass. Lower connectance implies the existence of fewer trophic pathways and feedback mechanisms, such as omnivory. This results in less stability in terms of population variability over time [170], with individual populations still fluctuating even after total community biomass stability was achieved after the invasion. This mirrors recent experimental work on the relationship between diversity and stability in competitive communities [252, 97]. In those studies diversity may stabilize aggregate community or ecosystem properties while simultaneously destabilizing individual species abundances. The possible mechanisms behind this apparently paradox are numerous, from compensatory dynamics that generate negative covariations in species abundances to stochastic processes that highlight the asynchrony in species responses to environmental fluctuations [138]. In our case, the exact mechanism is not clear, but it is likely related to the number and position of different trophic pathways, as w e model food webs, not single trophic level competitive communities. Further theoretical research could explore why, from a stability perspective, food webs with low connectance show similar dynamics to those displayed by highly diverse competitive communities.

4.4.1 Novel food webs resulting from invasions

Although widely recognised to have detrimental effects on ecosystem functioning and population abundances (e.g. [235]), the effect of invasions on community structure and organisation has been less explored. Theoretical and empirical work has shown, however, the effects of other components of global change in the structure of food webs, including climate change [144], habitat modification [254], and biodiversity loss [238, 72].

One of the main consequences of invasions in our complex model food webs was biodiversity loss, which in turn prompted important changes in food web structure. These network-level changes might be linked to those caused by the cascade of biodiversity loss that follows primary extinctions linked to the invasion event. Our post-invasion model communities became more connected, less modular, more homogeneous in terms of diet breadth, and with a smaller fraction of basal species. These novel features are similar to those that we identified to make communities more susceptible to invasions, showing that biodiversity loss makes communities more vulnerable to further perturbations [251, 31].

A homogenisation in terms of diet breadth and a decrease in the fraction of basal species affect the number of energy input channels in the food web. Fewer basal species are available for species in higher trophic positions, and most of the latter are generalists (since post-invasion communities are also more connected). This decreases the energy available and generates more competition for existing resources. Novel communities resulting from invasions are not only becoming less diverse in terms of species and interactions but are potentially resulting in higher levels of competition among the remaining species.

In summary, biological invasions are modifying species interaction patterns, eventually resulting in novel communities characterized by new properties. The direction and magnitude of such modifications are similar to those related to other components of global change, like climatic warming [193, 48, 144]. To what extent invasions and climate change act synergistically modifying food web structure and dynamics requires further integrative investigations.

4.4.2 Species traits and biological invasions

Several species traits have traditionally been proposed as determinants of invasion success. In agreement with recent empirical work (e.g. [27]), we found that body size and ability to capture prey are important determinants of invasion success. Propagule pressure, however (considered here as the biomass at the time of introduction), one of the most important predictors of invasion success in several empirical studies [109], did not affect invasion success in our theoretical approximation. This might be due to our choice of biomass ranges at the time of introduction, as we used biomasses within the range of those of the species present in the community. In combination, previous empirical studies and our theoretical result suggest that if the introduced species has a population size above some threshold (e.g., similar to native species), then the exact number of individuals at the time of introduction is no longer determinant.

Contrary to theoretical expectations, predation release does not seem to be a relevant mechanism behind the success of invasive species. This highlights the importance of a more comprehensive view of biological invasions in complex food webs. When considered in isolation, predation release might seem like a strong determinant of invasion success. However, when the wider food web is considered and other factors are taken into account, some of these factors may overpass the importance of predation release, like body size or ability to capture prey.

4.4.3 Limitations of our approach

Our work highlights the importance of comprehensive theoretical approximations that focus on multispecies systems to the study of biological invasions to understand the likely effects of these invasions on community structure and organisation. In spite of its advantages as a framework for community analysis, the present approximation has certain limitations. The main limitation is that certain ecological aspects that are thought to influence invasion success are not explicitly contemplated, including habitat suitability or competition for space. Our focus is on biotic interactions and some simplifications had to be necessarily made in order to keep the experiments manageable. We limited species interactions to antagonistic consumer-resource trophic interactions. Species can interact through many other types of interactions like competitive or mutualistic. As some works have suggested (e.g. [222, 6]), invasive species might find a beneficial setting provided by resident species through mutualistic interactions. These facts highlight the need to integrate facilitative interactions into the investigation of the effects of community structure and biotic interactions on invasions and vice versa.

Appendix

4.A Additional statistical results

Web property	**Coefficient**	*z*
C***	15.7132	4.632
L/S***	0.30768	5.209
MFCL***	0.48526	6.635
log(ChnNo)***	0.7860	6.209
GenSD***	-2.6862	-3.565
VulSD	-1.6502	-1.55
%B***	-8.6706	-5.381
%I***	6.5056	6.009
%T***	-5.9337	-3.80
Modularity***	-6.1296	-4.966

Table 4.A.1: Statistical results of GLMs testing the effect of food web properties on invasion success. Positive coefficient values indicate a positive relationship between the network property and invasion success, while negative values indicate a negative relationship. Degrees of freedom for the GLMs were 1046. *** indicates the p-value of the model for that variable was < 0.001.

Web property	**D**	***p-value***
C	0.1512	< 0.001
L/S	0.0402	0.4302
MFCL	0.0539	0.1279
log(ChnNo)	0.0856	0.002
GenSD	0.3436	< 0.001
VulSD	0.0687	0.023
%B	0.2526	< 0.001
%I	0.148	< 0.001
%T	0.0761	0.008
Modularity	0.0863	0.002

Table 4.A.2: Statistical results of Kolmogorov-Smirnov tests testing for differences in the distributions of food web properties values before and after invasion.

Pairwise comparison	Coefficient	z
C = 0.05 vs. C = 0.1 ***	0.87553	9.312
C = 0.05 vs. C = 0.15 ***	1.33927	11.310
C = 0.1 vs. C = 0.15 ***	0.46374	3.484

Table 4.A.3: Statistical results of pairwise comparisons (using GLMs) between the effects of body size of the invasive species on invasion success for the 3 different values of connectance used in this study. *** indicates the p-value of the model for that comparison was < 0.001

Pairwise comparison	Coefficient	z
C = 0.05 vs. C = 0.1 ***	0.9870	7.676
C = 0.05 vs. C = 0.15 ***	1.6722	9.830
C = 0.1 vs. C = 0.15 ***	0.6852	3.660

Table 4.A.4: Statistical results of pairwise comparisons (using GLMs) between the effects of of the ability to capture prey (hill exponent) of the invasive species on invasion success for the 3 different values of connectance used in this study. *** indicates the p-value of the model for that comparison was < 0.001

Pairwise comparison	Coefficient	z
C = 0.05 vs. C = 0.1 ***	0.8995	10.061
C = 0.05 vs. C = 0.15 ***	1.4176	12.688
C = 0.1 vs. C = 0.15 ***	0.5181	4.189

Table 4.A.5: Statistical results of pairwise comparisons (using GLMs) between the effects of diet breadth of the invasive species on invasion success for the 3 different values of connectance used in this study. *** indicates the p-value of the model for that comparison was < 0.001

Chapter 5

Diversity of interaction types mediates community stability on spatial ecological networks

Miguel Lurgi, Daniel Montoya, José M. Montoya

In preparation to submit to Ecology Letters

Abstract

Biodiversity and species interactions have traditionally been considered key elements for understanding ecosystem stability and functioning. One of the biggest challenges of complexity-stability relationships in ecological networks consists on exploring how interaction networks with different architectures and interaction types combine to shape the broader network that links together all the species in a community and what are the implications of this to community stability. In this chapter, we investigate the stability of "networks of networks" that combine antagonistic and mutualistic consumer-resource interactions within a spatially explicit context using an individual-based, bio-energetic model. We look at how different dimensions of ecological stability are influenced by the proportion of mutualistic vs. antagonistic interactions within the overall species interaction network. We find that increasing levels of mutualisms result in more stable communities in general, but different fractions of mutualistic interactions influence multiple dimensions of stability in different ways. Stability is either not influenced by mutualistic interactions -in the cases of population-level temporal variability and species' spatial distributions- or is positively influenced by them -spatial aggregation of species distribution, and distribution of interaction strengths. This work extends previous studies on the stability of communities with a mixture of interaction types by considering space explicitly and hence, by adding further dimensions to community stability analysis.

5.1 Introduction

Biodiversity and species interactions have traditionally been considered key elements for understanding ecosystem stability and functioning [150, 130, 202, 151, 139]. Research on the relationship between network architecture and community stability has shown that, whereas high connectance (the number of realised links) and nestedness promote stability in communities made up exclusively of mutualistic species and interactions, the stability of trophic networks is higher in modular and weakly connected architectures [249]. Although these studies have improved our knowledge on complexity-stability relationships in ecological networks, they usually focus on a single interaction type at a time and overlook the fact that natural communities comprise interactions types that operate simultaneously [79, 116]. Recent empirical work has already addressed the incorporation of different interaction types into a broader ecological network context, in which the creation of a network of networks and its implications for different aspects of community organisation are considered [156, 189, 79, 116].

One of the biggest challenges of complexity-stability relationships in ecological networks consists on exploring how interaction networks with different architectures and interaction types combine to shape the broader network that links together all the species in a community, and how this relates to the functioning and stability of ecosystems [249]. Recent attempts to do so have shown that interaction type may affect community stability and its relationship with network architecture [3], and that the proportion of trophic and mutualistic interactions may influence the stability of natural communities [172]. To date, the only study that explores how different proportions of antagonistic and mutualistic interactions affect the stability of the global community is that of Mougi & Kondoh in 2012 [172]. In that work, the authors developed a theoretical model of interaction networks including Lotka-Volterra predator-prey population dynamics with various combinations of mutualistic and antagonistic interactions. They concluded that, whereas the presence of a few mutualistic interactions destabilises predator-prey communities, a moderate mixture of antagonistic and mutualistic interactions could have a stabilising effect in 'hybrid' communities. We extend these findings by including an important aspect of community organisation, and that has been shown to play a crucial role for the stability of ecological communities: space.

The role of space in shaping communities and the interactions among their constituent species has been long recognised in ecology [147, 271], although its inclusion in ecological network studies happened at a later stage. Recently some other authors have recognised the stabilising effect of space for community dynamics [102, 154, 237]. These studies have shown that many patterns that we observe in nature, such as spatial distribution of species and percolation thresholds, can be understood only if we consider that natural populations move and interact in a spatial context. At present however, the inclusion of space into the complexity-stability debate in ecological networks is lacking.

Essentially, models with explicit space include the range of dynamics found in spatially implicit models but with greater restrictions to movement and species interactions. This affects the spatial distribution and the mobility of species in the community, which in turn modulates the dynamics of interacting species due to the probability of encounter between individual predators and prey [188, 42] and determines the realisation of potential interactions. For instance, two species in a community that can potentially interact might not do so simply because they do not encounter each other in space, a result of their different spatial distributions, abundance, and local dispersal abilities. Restrictions imposed by space are thus not only fundamental to understand patterns of diversity, but also spatial processes alone can result in network architectures that resemble those observed in real networks [168]. Spatial processes can therefore affect the stability of the community via the shaping of the network of interactions between species in the ecosystem, which in turn affects community stability. Also, spatial organisation allows for the assessment of community stability from new perspectives, which are more related to the changes of populations throughout their distributional ranges. Ecological stability has several components. It has been argued that including different metrics of stability would benefit the exploration of complexity-stability relationships [66]. The spatial component allows thus for a more comprehensive exploration of the relationship between network architecture and community stability.

In this chapter, we investigate the stability of "networks of networks" that combine antagonistic and mutualistic consumer-resource interactions within a spatially explicit context using an individual-based, bio-energetic model. We ask whether different dimensions of ecological stability are influenced by the proportion of mutualistic vs. antagonistic interactions (hereafter MAI ratio) within the overall species interaction network. Our aim is to explore the relationship between hybrid network architecture and community stability not only in terms of population dynamics but also including spatial stability. In this way we will be able to understand at the same time how space influences the stability of hybrid communities and how the architecture of these hybrid communities influences different dimensions of stability. Specifically, we address the following questions: (1) do increasing levels of mutualism result in more stable communities? If so, (2) how MAI ratios influence community stability in a spatial context? We expect to find stable communities due to the effects of space and also a strong relationship between MAI ratios and the stability of model communities. This represents a step further from previous work (e.g. [172]) because of the focus on communities with more realistic values of connectivity, on local interactions occurring at the individual level, and the consideration of space explicitly.

5.2 Methods

We developed and individual-based, spatially explicit, bio-energetic model of species interaction networks. Network architecture was obtained using the niche model [272]. The dynamics of the system are governed by local rules of interactions between individuals in a simulated, spatially-explicit, environment. Individuals' state is determined by several bio-energetic constraints. In order to analyze the model outcomes we employ several network metrics that are traditionally used for the characterisation of food webs and mutualistic interaction networks. Additionally, we also calculate different metrics of community stability to create a comprehensive picture of stability based on several dimensions. This model allows us to test the relationship between different mutualistic vs. antagonistic interactions (MAI) ratios and the network and stability metrics. We ran 25 replicates of experiments consisting of model communities generated using different MAI ratios and letting them evolve through time.

5.2.1 Generation of species interaction networks

Food web architecture of model communities was obtained using the niche model [272]. This model requires 2 input parameters: the number of species (S), and connectance, defined as the fraction of realised links ($C = L/S^2$) within the network. It is based on an algorithm that arranges species in a one-dimensional 'niche' and assigns predator and prey links to each species in the network in a hierarchical way. While several modifications of the niche model have been described [47, 244, 1], we chose the original niche model because it is able to approximate well the central tendencies and the variability of a number of network properties [272, 73, 244] while posing a small number of constraints on the definition of species interactions. The model for network construction selected however, should not affect our results, as long as realistic food web architectures are produced.

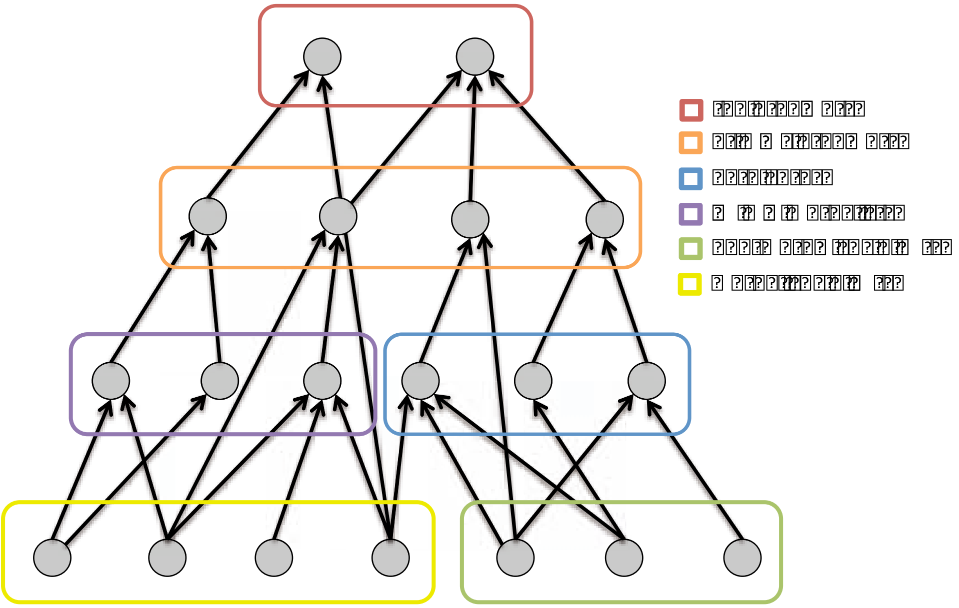


Figure 5.1: Schematic representation of the species interaction networks generated. Nodes correspond to taxonomic species and arrows to trophic links from resources to consumers. The six different categories of species, according to their position in the overall ecological network, that result from the process of network generation are shown (see text).

The niche model describes trophic niche occupancy between consumers and resources along a resource axis. Because of this, it can be applied to other types of consumer-resource interactions (aside from antagonistic predator-prey). We then used that same heuristic to define mutualistic plant-pollinator interactions, simply by substituting herbivory by mutualistic links while keeping connectance and species richness constant.

We created food webs comprising 60 species and with connectance values of 0.08. Once a food web was generated in this way, and in order to obtain a ‘hybrid’ interaction network, some links in the network, among those specifying interactions between basal species and species in the first trophic level (i.e. herbivore links) were selected to become mutualistic links according to the corresponding MAI ratio. The MAI ratio hence corresponds to the proportion of plant herbivores vs. plant mutualists in our networks. We generated networks with this characteristics for MAI ratios ranging from 0 to 1.0 with steps of 0.1: [0, 0.1, 0.2, 0.3 ... 1], making up a total of 11 different MAI ratios, from communities with no mutualistic interactions to communities with only mutualistic links and no herbivores.

Our approach for creating the interaction networks ensures that mutualistic partners (both animal and plants) are embedded in a whole community context alongside other trophic groups such as omnivores and top predators. It also ensures that a trophic pyramid is maintained within the community, with mutualistic interactions sitting at the bottom of the pyramid, between basal species and primary consumers. In summary, this method creates a network architecture that is consistent with food webs while at the same time allowing for a well-identified section composed of mutualistic interactions, from which network properties that are exclusive of mutualistic networks can be calculated. The resulting species can thus be classified into 6 categories according to their position within the overall food web: (1) non-mutualistic plants, (2) mutualistic plants, (3) animal mutualists or mutualistic consumers, (4) herbivores, (5) primary predators, and (6) top or apex predators (figure 5.1).

5.2.2 Individual-based spatially explicit dynamics

Individual-based models (IBMs) have been used to tackle different problems in ecology, although not very frequently to simulate complex ecosystems comprising large numbers of species [88]. We implemented an IBM that simulates dynamics typical of two-dimensional cellular automata (CA) [266, 276] although based on ecological rules of interaction. This CA represents thus our simulated ecosystem: a two-dimensional grid of cells in which each cell can be occupied at a given time by at most two individuals belonging to a given species in our model communities. Individuals change their state (or not) at every iteration of the model, not only according to their interactions but also as a function of a number of bio-energetic constraints summarised below.

All individuals in the IBM are equipped with an energy storage unit. This energy is the currency governing the actions performed by individuals, their lifespan, and the mean by which the economy of the whole artificial ecosystem is maintained.The rules of this complex CA simply represent the demographic processes, foraging actions, and inter/intra -species interactions of individuals in our IBM. Thus, the basic processes that occur at the individual level are:

1. ***Death***: Individuals possessing less than a fixed number of energy units die and are removed from the system.

2. ***Movement***: Individuals can move to one of its 8 neighbouring cells (see figure 5.2) chosen randomly, provided that it is available.

3. ***Reproduction***: Individuals can reproduce using one of two strategies given that they have enough resources (i.e. energy) to do so (see table 5.1 for parameter values):

    (a) *Sexual reproduction* occurs between individuals of the same species that are not basal species. Only if both individuals are occupying neighbouring cells reproduction happens.

    (b) *Asexual reproduction* occurs in basal species (i.e. plants), and in this case it happens either through ‘wind dispersal’, in which case the spatial extent of the dispersal event is defined by the neighbourhood of the subject individual, or through mutualistic dispersal. In the latter case, dispersal is done by the animal partner, which means that the ‘seed’ for a new individual can travel farther before it settles. The spatial extent of this dispersal event will depend on the movements of the animal disperser after it has visited a mutualistic plant partner, its efficiency in dispersing the ‘seed’, and a cooling effect that decreases the dispersal efficiency as time lapses (see table 5.1 for parameters governing this behaviour and their explanation). Plants do not reproduce sexually in our model because we do not need to simulate genetic processes (e.g. recombination) but only the ecological fact that they can reproduce without physically encountering an individual of their same species.

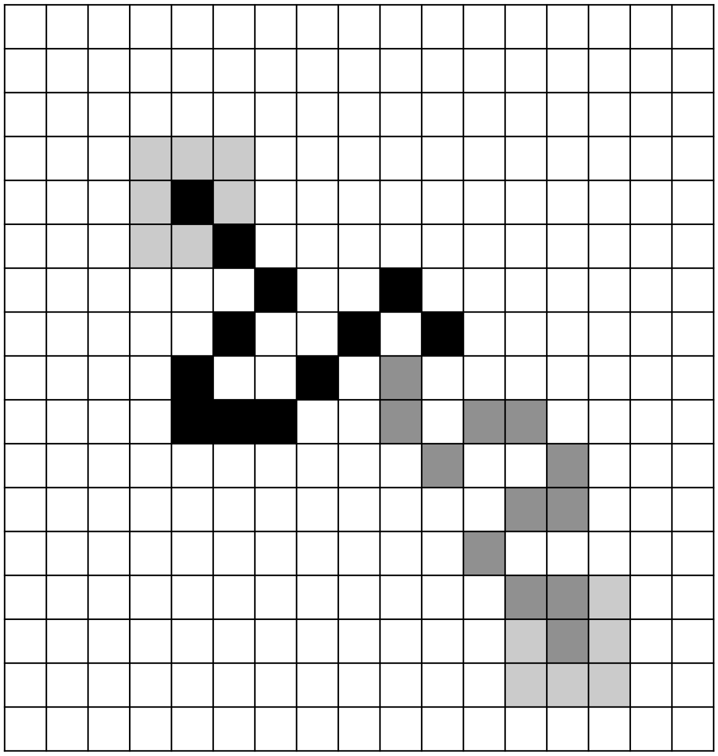


Figure 5.2: Example of a 2D grid (17x17 cells) representing the ecosystem where the digital organisms in the individual-based model co-exist and interact. The trajectories of two sample individuals until they encounter each other are represented by black and dark grey squares. Light grey squares represent the neighbourhood of each of the two individuals at the beginning of their respective current paths. At the end of both paths, each individual finds itself inside the other's neighbourhood. Depending on other individuals present on a given individual's neighbouring cells (shown as light grey cells for the starting position of each of the two individuals in the figure) or whether these are available, the 'state' in this complex cellular automaton will change following certain rules and constraints (see text).

4. ***Feeding***: This is perhaps the most fundamental mechanism of the model. It occurs when two individuals of species that are linked via a potential interaction defined by the niche model find each other in space (i.e. one is occupying the cell that it was chosen by the other when moving). Several outcomes are possible:
   (a) If both are non-basal species a predation event occurs, in which the prey dies and the predator increases its energy storage unit's level.
   (b) If one individual is a basal species and the other is a non-mutualistic primary consumer, then the herbivore takes some resources from the plant and both continue living.
   (c) If it is a mutualistic relation, the animal takes resources from the plant it visits while at the same time 'keeping track' of the species it belongs to until some point in the future. If, before this time lapses, the animal partner comes across an empty cell in the world, it 'creates' an offspring for the plant previously visited with a probability given by the mutualistic efficiency (see table 5.1).

In all cases an efficiency or assimilation rate of resources is applied. This coefficient differs between herbivore and carnivore links, since assimilation varies depending on whether the food is plant material rather than animal material (see table 5.1 for parameter specification) [105].

In addition to the demographic processes specified by the previous rules, the model incorporates immigration, which is simulated by each empty cell on the grid having a probability (see table 5.1) of accepting a new individual from a randomly chosen species from the original species pool (i.e. a species from the original ecological network).

The macroscopic dynamics of the CA emerge thus from the local interactions occurring between individuals occupying cells in the 2D grid (figure 5.2). These dynamics will determine not only the spatial distribution of species in the grid (states of the CA) but also the population dynamics of each species through time. Persistence/extinction dynamics in the community are described in terms of energy efficiency and storage at the individual level (see table 5.1 for description of bio-energetic parameters), rather than assigning extinction probabilities drawn from some probability distribution to all species in the community (e.g.[239, 81]).

Each iteration or time step in the simulation without an interaction event will reduce the energy storage of the every individual due to metabolic losses. This loss of energy, without replenishment via feeding interactions, will make more difficult the individual's reproduction, since reproduction demands an investment of energy, and will eventually cause the extinction of that individual.

With the exception of efficiency transfer coefficients, bio-energetic parameters are identical for all species in the ecosystem (see table 5.1 for a full list of parameters). This individual-based bio-energetic model is more realistic than previous models commonly used to simulate food webs dynamics at least in the following aspects: (i) individuals within species have different extinction rates, which are not dependant on stochastic events, eliminating in this way the need to define fixed extinction probabilities for all species in the community; (ii) more complex demographic processes such as reproductive ability, and immigration based on available space, are taken into account; and (iii) bio-energetic constraints such as energy gathering efficiency, and energy loss at the individual level are the driving processes behind the dynamics of populations.

Spatial communities evolve through time following constraints imposed by bio-energetic parameters (see table 5.1), spatial constraints (similar to all individuals), and the interactions between species specified by the network architecture (figure 5.3). Potentially interacting species, as defined by the interaction network, interact if individuals belonging to species linked together in this web are nearest neighbours in the 2D grid. After 5,000 time steps, which include an initial period of transient dynamics, the communities are analysed in terms of diversity (species richness and abundances), network properties [272, 21, 29], and stability.

5.2.3 Food web properties and community diversity

Several statistical properties of the network of species interactions were measured after transient dynamics. In particular, we measured the number of species in the network (S), number of links or ecological interactions (L), connectance -i.e. the fraction of realised out of the possible links in the network ($C = L/S^2$)-, the standard deviation of generality (GenSD) -a measure of diet breadth variability across species-, and the standard deviation of the vulnerability (VulSD) -a measure of predation pressure variability across species [272].

We also calculated metrics for extracting information about the organisation of links over the whole ecological network, such as compartmentalisation: an aggregated measure over all

Parameter name	**Value**	**Description**
OCCUPIED_CELLS	0.4	Fraction of the grid initially occupied by individuals randomly placed on it.
MAX_RESOURCE	20	Maximum amount of resource an individual may possess at any given time.
MIN_RESOURCE	3	Death threshold: minimum amount of resource at individual may possess. Any individual possessing less than this amount at any given iteration will die (see text).
LIVING_EXPEND	0.01	Fraction of resource an individual spends in living every iteration of the model. Metabolic rate.
MATING_RESOURCE	0.5	Fraction of MAX_RESOURCE that is required for an individual to be able to reproduce.
MATING_ENERGY	0.2	Fraction of resource given to the offspring by the parent during reproduction. Each parent gives the same fraction. The total amount depends on how much resource the parent possesses at the time of reproduction.
IMMIGRATION	0.005	Probability that a new individual will appear in a cell of the grid in each iteration. The species this individual belongs to is randomly chosen from the original species pool.
SYNTHESIS_ABILITY	0.1	Fraction of resource that is autotrophically created by each individual from the basal species every iteration. This is the only energy input to the system.
HERBIVORY_FRACTION	0.7	Fraction of resource lost to herbivores by individuals belonging to a basal species during a trophic event, i.e. a species in the first trophic level feeding on a species in the basal level.
OMNIVORY_TRADEOFF	0.4	Fraction of resource that omnivores are effectively able to gather when feeding on a species from the basal level (e.g. a plant).
MUTUALISTIC_FRACTION	0.25	Fraction of resource of a primary producer (basal species individual) that a mutualistic partner obtains when an interaction of this type occurs.
CAPTURE_PROB	0.4	Probability that a predator individual embark upon a trophic relationship with one of its prey individuals when it encounters it.
EFFICIENCY_TRANSFER	0.2	Fraction of the resource the prey that is assimilated by the predator in a carnivorous interaction, i.e. trophic interaction not involving individuals from the basal species.
HERBIVORY_EFFICIENCY	0.8	Fraction of the resource of the prey assimilated by the herbivore in an herbivorous interaction.
MUTUALISTIC_EFFICIENCY	0.8	Efficiency of an individual mutualist when dispersing a plant partner. In other words, the probability with which a mutualistic individual will facilitate the creation of a new individual of the last species of plant it visited when it is positioned on an empty cell immediately after it interacted with a mutualistic plant partner.
MUTUALISTIC_COOLING	0.9	Cooling factor for the mutualistic efficiency of plant dispersers (mutualists). This is the fraction of mutualistic efficiency that remains after each iteration.
REPRODUCTION_RATE	0.01	Reproduction rate of non-mutualistic plant species. Probability with which an individual belonging to a plant species that does not possess mutualistic partners for dispersal will create an offspring in any given iteration of the simulation run.

Table 5.1: Parameters for the model described in the text, including bio-energetic values.

the nodes/species on the network that quantifies the fraction of shared partners between pairs of species (as presented by Pimm and Lawton in [206]); and exclusively over the mutualistic part of the web such as nestedness: a measure of the degree to which the diets of mutualistic

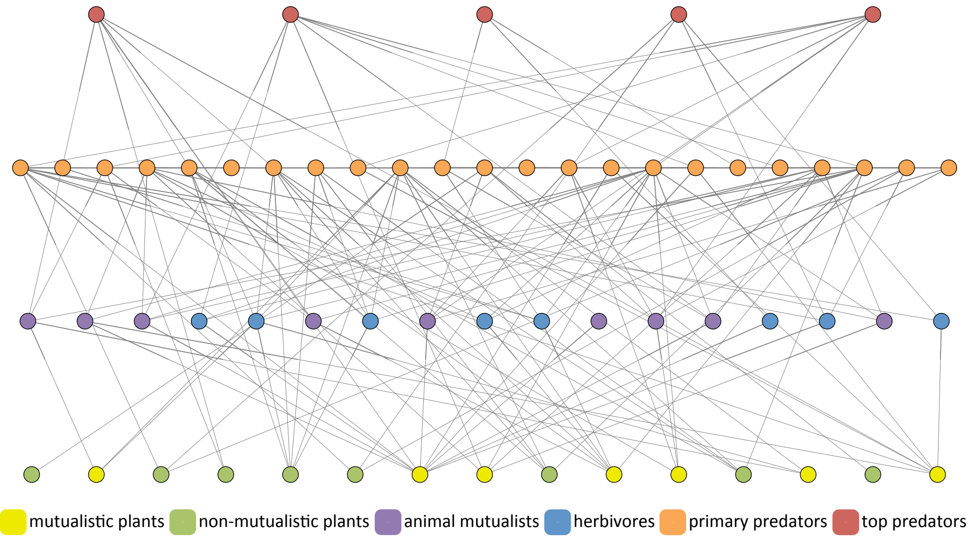


Figure 5.3: Example of the overall network of ecological interactions taken from one of the model communities analysed in this study. Nodes represent species, while links (lines) are trophic or mutualistic relationships amongst them. The colour of the nodes represent the group the species belongs using the same reference as in figure 5.2. Thicker part of the line shows the end of the link. Links go from resource to consumer species. The layout orders species per trophic level with higher trophic levels towards the top of the diagram.

consumers are proper subsets of other, more generalist, ones.

Additionally, we obtained quantitative metrics based on the strength of interactions between species including: $H_2^{'}$ -a measure of mutualistic specialisation- [29], which was calculated over the mutualistic part of the web; and quantitative measures of generality and vulnerability, G_q and V_q [21] (see table 5.2 for specification of each metric).

In addition to properties related to network architecture, we also measured properties more commonly employed on the study of diversity in natural communities, such as the Shannon diversity and Shannon evenness indexes [16]. These indexes were measured not only at the community level but also within each of the functional groups specified in figure 5.1. The Shannon diversity index is defined as:

$$H^{'} = -\sum_{i=1}^{S} p_i \cdot ln\, p_i$$

where, as before, S is the number of species and p_i is the proportion of individuals of species i. When the index is calculated within functional groups the proportion of individuals is taken only considering the species within the group. Shannon evenness index on the other hand is calculated as:

$$J^{'} = \frac{H^{'}}{ln\, S}$$

5.2.4 Community stability

The stability of ecological communities has traditionally been assessed using tools borrowed from local stability analysis of dynamical systems [149]. Using local stability analysis May

Property	Formula
C: connectance, fraction of realised links out of the possible ones	L/S^2
GenSD is the standard deviation of the normalised number of prey G_i across species.	$G_i = \frac{1}{L/S} \sum_{j=1}^{S} a_{ji}$, where a_{ji} is 1 if there exists a trophic link between prey j and predator i, and 0 otherwise.
VulSD is the standard deviation of the normalised number of predators V_i across species.	$V_i = \frac{1}{L/S} \sum_{j=1}^{S} a_{ij}$, where a_{ij} is 1 if there exists a trophic link between prey i and predator j, and 0 otherwise.
Compartmentalisation is the degree to which species share common neighbours across the web [206]	$Comp = \frac{1}{S(S-1)} \sum_{i=i}^{S} \sum_{\substack{j=1 \\ j \neq i}}^{S} c_{ij}$, where c_{ij} is the number of species with which both i and j interact divided by the number of species with which either i or j interact.
Nestedness: the extent to which the diet of species is a proper subset of more generalist ones	Calculated using the nestedness metric based on overlap and decreasing fill (NODF) proposed by Almeida-Neto *et al.* [4]
$H_2^{'}$: two-dimensional standardised Shannon entropy, as proposed by Blüthgen *et al.* in [29].	$H_2^{'} = \frac{H_{2max} - H_2}{H_{2max} - H_{2min}}$, where H_{2max} and H_{2min} are the maximum and minimum H_2 for the particular network over which the index is being calculated (see [29] for details); and $H_2 = - \sum_{i=1}^{r} \sum_{j=1}^{c} (p_{ij} \cdot ln\, p_{ij})$, where r and c are resources and consumers in the mutualistic web respectively. p_{ij} is the proportion of the total number of interactions in the network that occur between resource species i and consumer species j.
G_q: weighted (quantitative) generality, as proposed by Bersier *et al.* [21].	$G_q = \sum_{k=1}^{S} \frac{b_{\cdot k}}{b_{\cdot\cdot}} n_{N,k}$, where $b_{\cdot k}$ is the total amount of biomass going into species k, and $b_{\cdot\cdot}$ is the total amount of biomass flowing through the entire food web. $n_{N,k}$ is the number of prey that predator k has. Here the biomass flowing from one species to another was calculated as the number of individuals of a given prey species eaten by individuals of predator species k.
V_q: weighted (quantitative) vulnerability, as proposed by Bersier *et al.* [21].	$V_q = \sum_{k=1}^{S} \frac{b_{k\cdot}}{b_{\cdot\cdot}} n_{P,k}$, where $b_{k\cdot}$ is the total biomass emanating from species k. $b_{\cdot\cdot}$ is the total biomass flowing through the entire food web. $n_{P,k}$ is the number of predator species that feed upon prey species k. Here the biomass flowing from one species to another was calculated as the number of individuals of prey species k eaten by a given predator species.

Table 5.2: Metrics applied over the interaction networks to obtain information about its structural and quantitative properties.

concluded that a complex ecosystem would be stable if, and only if, it complied with the following condition: $< i > (SC)^{1/2} < 1$, where $< i >$ is the mean strength of the interaction between species in the community - the strength of the interaction between species i and j is the effect of species i on the population growth rate of j. S and C correspond to the number of species in the community and its connectance, respectively.

We estimated the interaction strength between a predator j and its prey i as:

$$\alpha_{ij} = \frac{b_{ij}}{N_i * N_j}$$

where b_{ij} is the total biomass flowing from prey species i to predator species j -quantified here as the total number of individuals (or fractions of it, in the case of plants) from species i eaten by individuals of species j-, and N_i and N_j are the total number of individuals of species i and j at the time of the calculation of the index, respectively. This way of calculating interaction strengths quantifies the per-capita effect of a predator species over its prey, and it is thus analogous to Paine's index and Lotka-Volterra interaction coefficients [175, 20]. This allows us to employ these values to assess and understand community stability using Mays approach.

In contrast to previous theoretical studies on the relationship between network architecture and stability of hybrid communities, where stability is usually defined as the proportion of stable communities following May's criterion (e.g. [3, 172]), all our simulated communities were dynamically stable (i.e. $< i > (SC)^{1/2} < 1$). Therefore, stability in our communities is based on a more quantitative approach, i.e. how more or less stable are communities that are qualitatively stable as defined by May's criterion.

In addition to local stability, we further measured 3 different types of community stability. First, temporal variability, which quantifies population variability as the average of the coefficient of variation (CV) in species population abundances through time [202]. Second, spatial variability, which corresponds to the coefficient of variation in the location of the centroid of each species' range (see below). And third, aggregation stability, measured as the clustering degree of individuals within each species (i.e. Moran's I and Geary's C indexes described below). Under these criteria, more stable communities will be characterised by lower temporal and spatial variability, higher reproductive stability, and lower average interaction strengths.

The centroid of each species population was calculated as the average of the positions of all the individuals belonging to that species in the 2D grid. It is thus a measure composed of two values: x and y coordinates for the average of the locations. Moran's I and Geary's C are metrics commonly used for the quantification of spatial correlation or 'aggregation' in spatially explicit data [80]. Moran's I for a given species is defined as:

$$I = \frac{N}{{}_i \quad {}_j \, \omega_{ij}} \frac{{}_i \quad {}_j \, \omega_{ij}(X_i - \bar{X})(X_j - \bar{X})}{{}_i (X_i - \bar{X})^2}$$

where N is the number of spatial units indexed by i and j, cells in the 2D grid in our simulated world; X is the variable of interest, which takes the value of 1 if an individual of the species for which the index is being calculated is present in that cell and 0 otherwise; $\bar{X}$ is the mean of X; and ω_{ij} is an element of a matrix of spatial weights. In our case, the weights of this matrix are always 1 because all the cells in the grid are equally important for the calculation of the index. Geary's C is defined as:

$$C = \frac{(N-1) \quad {}_i \quad {}_j \, \omega_{ij}(X_i - X_j)^2}{2W \quad {}_i (X_i - \bar{X})^2}$$

where in addition to the values defined for the Moran's I, we also have W, which is the sum of all ω_{ij}; in our case, the number of cells in the grid. These two indices are used to quantify spatial aggregation at the global (Moran's I), vs. spatial aggregation at the local (Geary's C) scale, and are therefore complementary ways of quantifying spatial aggregation.

We explore the relationships between network properties and the stability measures in our theoretical communities. More specifically, we are interested in how temporal and spatial stability changes as MAI ratio, and the network properties associated to it, increases. We expect to find that communities with a larger fraction of mutualistic interactions will be more stable in terms of the stability measures presented above.

5.2.5 Experimental simulations

We generated networks with 11 different MAI ratios, as specified above, in order to study the effects of different combinations of antagonistic and mutualistic interactions on community stability. The individual-based model described above was employed to carry on a series of simulations of the dynamics of the system through time and space. Simulations were set up by placing a given community, made up of artificial individuals belonging to each of the species in the interaction network defined by the niche model, on a landscape that consists of a 200x200 square lattice with identical cells. Each cell can be occupied at any given time by at most two individuals, yielding a maximum of 80,000 individuals. At the beginning of the simulations only 40 percent of the landscape was occupied and populated with the same number of individuals of each species randomly across the 2D grid. After the initial configuration, the state of each cell was evolved in a cellular automata-like manner through discrete time steps as described above, where each individual follows a set of rules according to its position in the food web, its position in space, and its current state and that of its neighbouring cells. Communities were let to evolve in for 5,000 iterations under constant monitoring where several properties of the community and its network of interactions were measured.

We performed 25 replicates for each of the 11 MAI ratios, each of them with representing different sets of initial conditions, not only in terms of the initial configuration of the simulated landscape but also regarding the network of interactions. For each of these 25 replicates the initial distributions of individuals across the landscape varied by placing individuals randomly across the landscape for each replicate as detailed above. The network of interactions for each of these replicates was generated independently by running different instances of the niche model with the same S (number of species) and C (connectance) values, and choosing the mutualistic links following the heuristic described above. This effectively produced different interaction networks for each run with the same number of species and connectivity. Each of the 25 communities simulated for each MAI ratio was thus independent and the architecture of the ecological network defining the interactions between its species was different from replicate to replicate. This yielded a total of 25x11 = 275 replicates.

Linear models (LM) were used to analyse the correlation between MAI ratios and the properties of the communities and their interaction networks detailed above. For comparing the distributions of interaction strengths we used Kolmogorov-Smirnov (KS) tests.The IBM used here was developed using Python v2.7 [257], while statistical analyses were done in R 2.15.2 [214].

5.3 Results

5.3.1 Community structure

After a period of transient dynamics the resulting simulated communities and their associated interactions networks display patterns similar to those found in natural communities. Population dynamics show oscillations typical of predator-prey and mutualistic interactions in multispecies systems, with all species in the community persisting through time. Rank-abundance plots display lognormal distributions (figure 5.1), typically found in natural communities [148]; and degree distributions that characterise the interaction networks follow an exponential pattern ($p < 0.001$ for all fits to exponential models) (figure 5.2), which has been observed in empirical food webs [162].

Diversity metrics changed as expected by an increase in MAI ratios. Level of mutualism does not affect total community species richness. Communities with larger MAI ratios, however, are composed of a larger number of individuals ($F_{1,9} = 98.12, p < 0.001$) (figure 5.3a). In spite of a decline in the abundance of non-mutualistic primary producers and herbivores with increasing MAI ratios (as expected due to a larger fraction of mutualistic species), the increase in mutualistic plants and animals overcompensates for this loss, causing an overall increase in the abundance of individuals in the community. This over-compensation is due to mutualistic plants becoming more abundant than non-mutualistic ones because mutualistic consumers do not consume as much resources from them and are actually beneficial for their reproduction; facilitating in this way the persistence and increase of mutualistic animals over herbivore numbers in communities with less mutualists.

Increased MAI ratios promote a general decline in Shannon diversity and evenness indexes, H (figure 5.3b) and J respectively, either measured at the community level ($F_{1,9} = 216.4, p < 0.001$) as well as those measured per functional group. This result is in line with our previous observation of an increased overall abundance of individuals because of a systematic increase in mutualistic plant and animal abundances. It suggests that the proportion of mutualistic species in the community has a profound effect on diversity, making model communities more biased towards mutualistic species.

Most network properties were not significantly affected by the degree of mutualism vs. antagonism. However, some of them did show a monotonic relationship with the MAI ratio. Quantitative generality (G_q) was significantly lower in communities with higher MAI ratio ($F_{1,9} = 96.87, p < 0.001$; figure 5.4a), whereas degree of specialisation ($H_2^{'}$) within the mutualistic sub-web decreased ($F_{1,8} = 38.43, p < 0.001$) -when this index increases specialisation decreases, see [29] for details- (figure 5.4b). These results combined indicate that a larger fraction of mutualistic interactions within the ecological network results in more generalised mutualistic interactions within a more specialised overall network. It is important to note that we are referring here to quantitative metrics. This means that, given a constant network architecture, interactions at the whole network level are getting weaker in general, with only a few interactions dominating. In the mutualistic sub-web, on the other hand, interactions are getting stronger in general. This might be a consequence of a reduction in the number of antagonistic interactions, since there are less potential antagonistic interaction partners (herbivores), which may be stronger interactors than mutualistic ones. Non-significant differences were observed in modularity, nestedness or connectance, for communities with differing MAI ratios, indicating that the arrangement of links within the network remained the same in spite of changes in the degree of mutualism within the network.

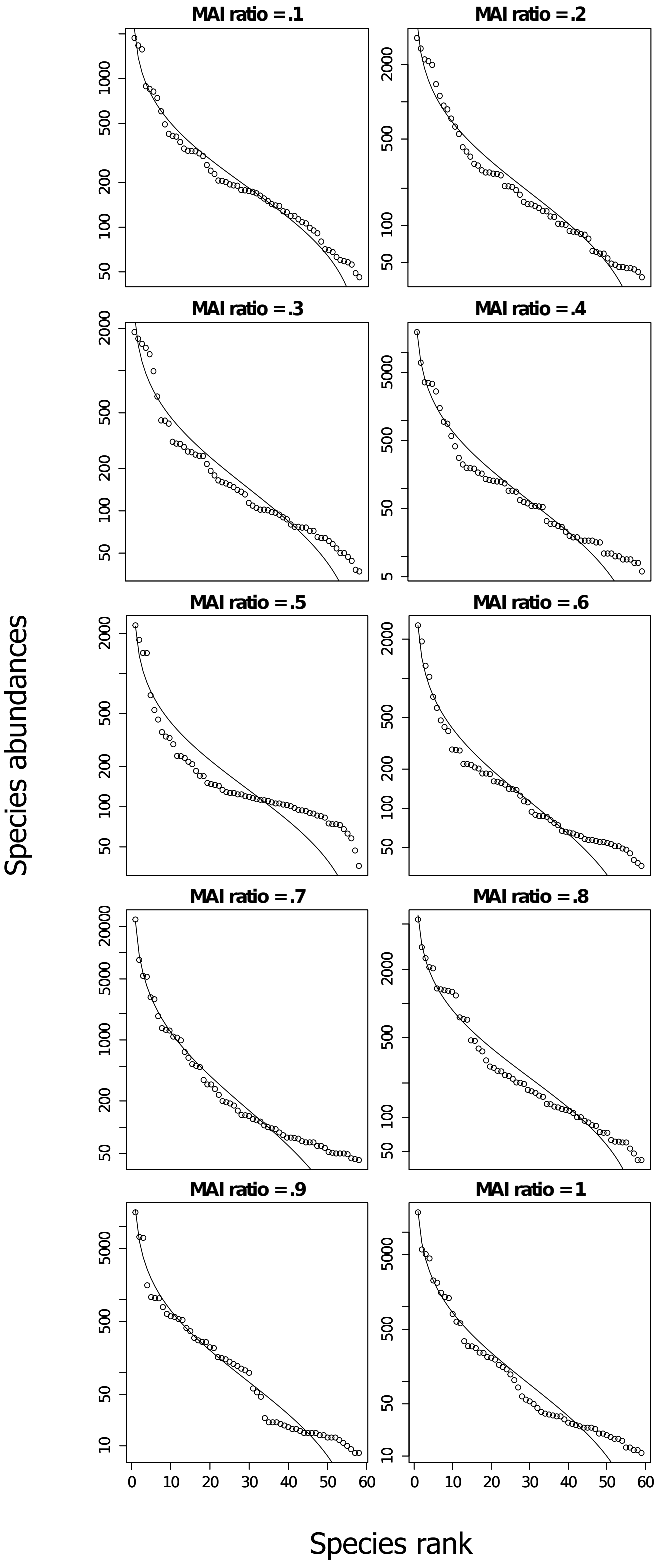


Figure 5.1: Rank-abundance distribution plots of 9 sample food webs with different MAI ratios and which are representative of the set of communities investigated here. Lines represent a fit of the data to a lognormal distribution, typically observed in empirical rank-abundance distributions [148].

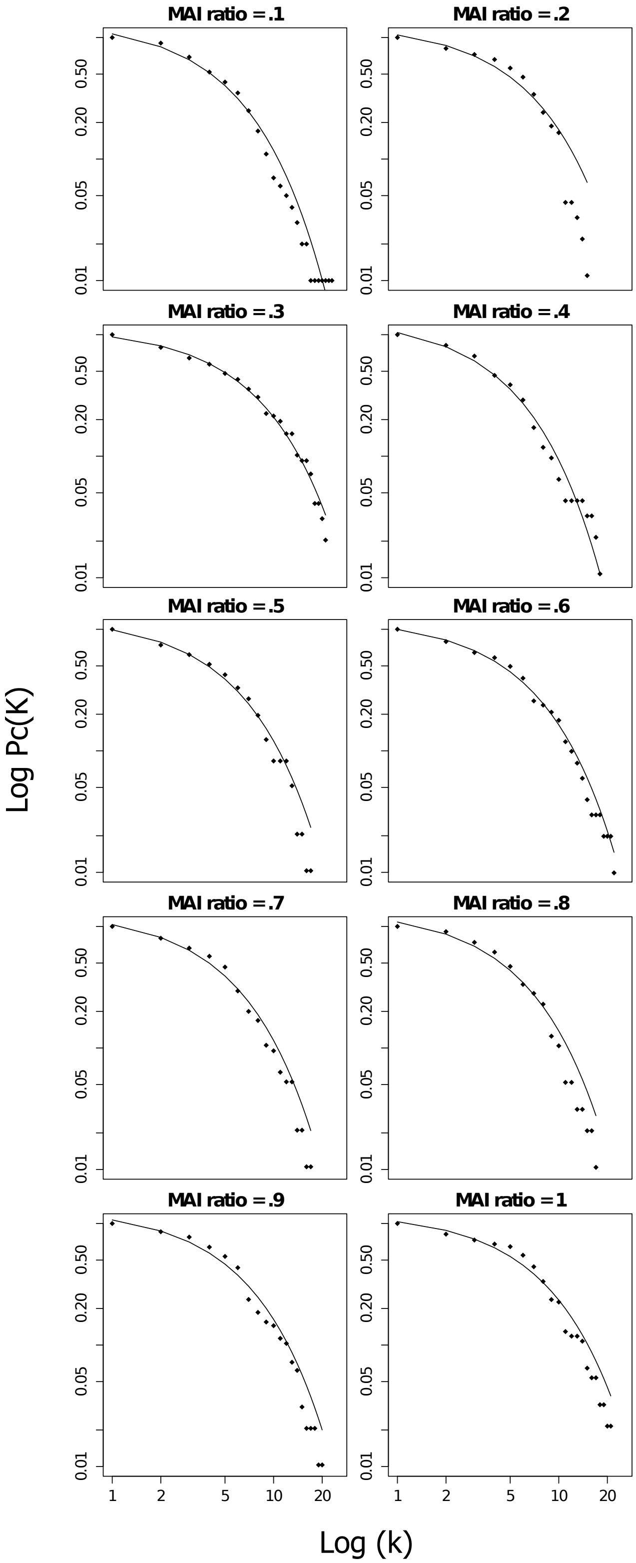


Figure 5.2: Cumulative degree distributions from 9 sample communities with different MAI ratios. k is node degree and Pc(k) the cumulative probability for $\geq$ k where P(k) is the probability a species has k links to other species in the network. Lines represent a fit of each dataset to an exponential distribution ($p < 0.001$ for all fits to exponential models).

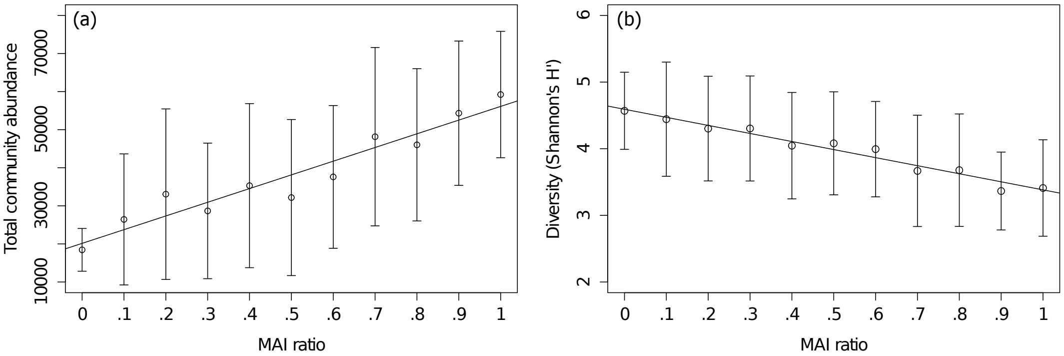


Figure 5.3: Abundances of individuals and Shannon diversity index at the total community level. (a) Total number of individuals vs. MAI ratio, (b) Shannon diversity index vs. MAI ratio. Points and bars along them on plot represent mean and standard deviation over 25 replicate communities, respectively. Lines represent the fit of a linear model for each data set (see text for statistics).

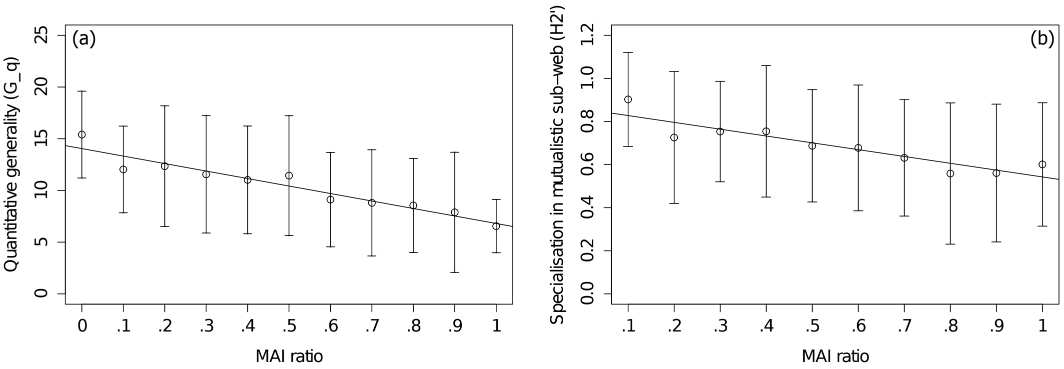


Figure 5.4: Quantitative generality (G_q) and degree of specialisation in the mutualistic sub-web $(H_2^{'})$ in the ecological network of the model communities analysed in this study vs. the MAI ratio. Points and bars along them on plot represent mean and standard deviation over 25 replicate communities, respectively. Lines represent the fit of a linear model for each data set (see text for statistics).

5.3.2 Community stability

All communities obtained were dynamically stable according to May's criterion ($< i > (SC)^{1/2} < 1$) [149]. MAI ratios affected different community stability measures in diverse ways. Communities with different proportions of mutualism and antagonism showed similar patterns in population variability through time, indicating that temporal population dynamics stability is not affected by MAI ratios. Spatial stability, as measured by the change in the centroid of the species' spatial range, as well as the area and density of species populations, were similarly unaffected by changes in MAI ratios.

In contrast, higher MAI ratios resulted in significantly higher and lower Moran's I ($F_{1,9} = 18.39, p < 0.01$; figure 5.5a) and Geary's C ($F_{1,9} = 15.39, p < 0.01$; figure 5.5b) indexes, showing more aggregated populations with increasing MAI ratio. More spatially aggregated populations are associated with higher reproductive stability since the likelihood of finding a reproductive partner in the neighbourhood is higher. Communities were thus more stable in

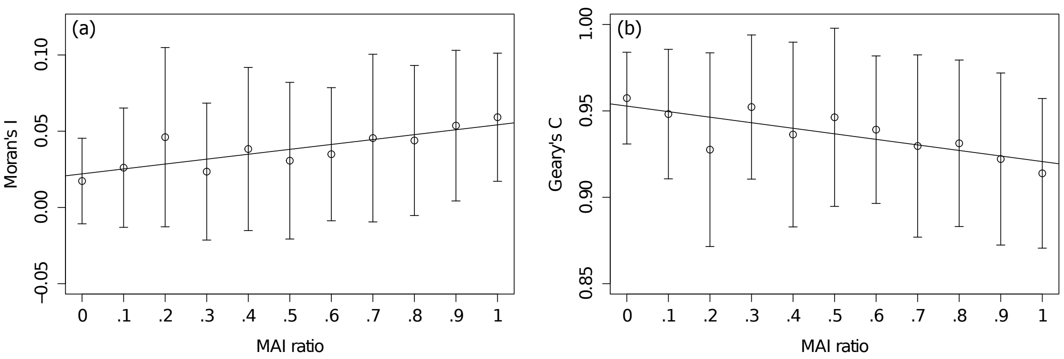


Figure 5.5: Moran's I and Geary's C vs. MAI ratio in the simulated communities analysed here. Points and bars along them on plot represent mean and standard deviation over 25 replicate communities, respectively. Lines represent the fit of a linear model for each data set (see text for statistics).

terms of species reproductive potential as the MAI ratio increased.

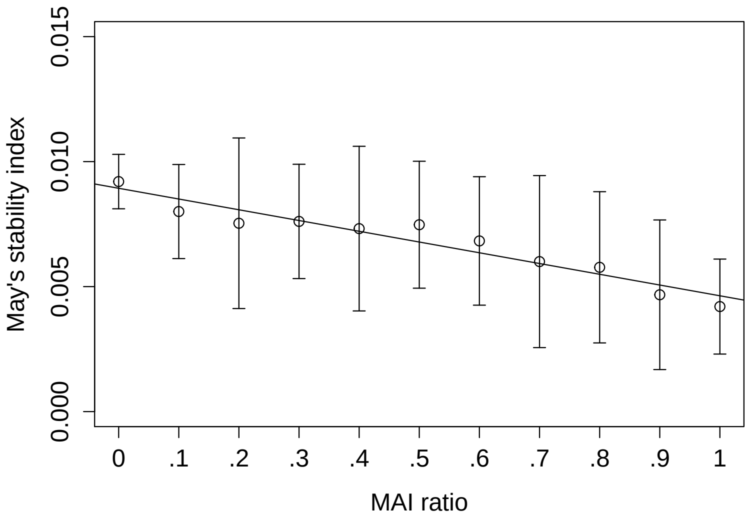


Figure 5.6: May stability index ($< i > (SC)^{1/2}$) vs. MAI ratio in the model communities studied in this work. Points and bars along them on plot represent mean and standard deviation over 25 replicate communities, respectively. Lines represent the fit of a linear model to the data set (see text for statistics).

Finally, even though all the simulated communities are dynamically stable according to May's criterion, we found that MAI ratios enhance May stability ($F_{1,9} = 104.6, p < 0.001$; figure 5.6). Because May stability is calculated taking into account species richness, connectance and average interaction strength; and since the two former variables did not change with MAI ratios, this result is a direct consequence of the reduction in the average interaction strength within communities with higher MAI ratios, yielding more stable communities. This result suggests that mutualistic interactions make communities more stable by lowering the average interaction strength between species.

When looking at the distributions of interactions strengths in communities with different

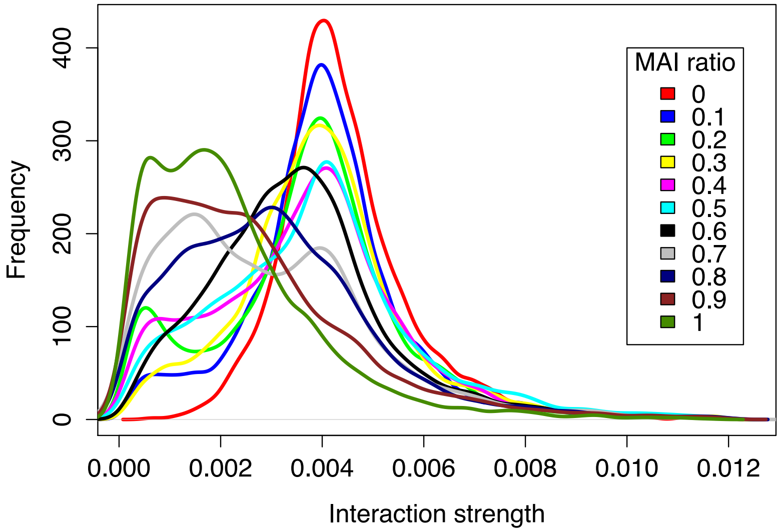


Figure 5.7: Frequency distributions of the strengths of the interactions in the overall ecological network across different values of the MAI ratio.

MAI ratios we find evidence for this. Our results show that interactions strengths distributions are shifting towards lower values as MAI ratio in the network of interactions increases (figure 5.7). The differences between these distributions are statistically significant ($p < 0.001$ for all pairwise comparisons between distributions). These result supports our previous finding on the decrease of the average interaction strengths in communities with higher MAI ratios (figure 5.6), suggesting that the mechanism behind the decrease in average interaction strength is in fact an overall shift of interaction strengths towards lower values.

Sensitivity analyses carried on showed that all the results presented here are independent of landscape size, number of species, and number of generated communities. Simulations were performed with lattice sizes of 50x50, 150x150, 200x200 (the value used for the simulations reported here), and 250x250; which demonstrated that for lattice sizes above 200x200 results are qualitatively and quantitatively similar. For smaller sizes (i.e. 50x50 and 150x150) some of the patterns observed varied quantitatively. Different values for the number of species in our communities were considered: 40, 60, 80, and 100. In this case, again, significant differences in community patterns were not observed between species richness values of 60 and greater. Experiments were performed considering 25, 50, and 100 replicates of communities for a subset of the MAI ratios studied here. We found no statistically significant differences between results obtained for these three values. We chose the smaller lattice size, number of species and number of replicates that better allowed us to obtain the most accurate results in order to save in computation time. Trade-offs needed to be done between computation costs and size of the experiments.

5.4 Discussion

Recent empirical work has devoted considerable effort into the inclusion of different interaction types into a broader and more realistic ecological network scenario that needs further theoretical explorations (e.g. [156, 189, 79, 210]). Central ecological debates, as that of the relationship between network complexity and community stability [150, 202, 151] must be revisited using different interaction types at the same time. Few studies have addressed this issue from a theoretical perspective [249, 3, 172] and have found that the balance between mutualistic and antagonistic interactions is a strong determinant of community dynamics and stability. Purely mutualistic architectures tend to be unstable from a local stability analysis perspective [3, 172], even when they have been shown to be key for minimising competition and hence increasing biodiversity by coexistence in mutualistic communities [14]. A mixture of mutualistic and trophic interactions, on the other hand, might be able to confer higher levels of stability to complex ecological communities [172].

In this chapter we delve deeper into the study of the relationship between different mixtures of interaction types and community stability in order to investigate whether and how the fraction of mutualisms within the network of ecological interactions between species in complex communities influences their stability. Increasing levels of mutualisms result in more stable communities in general. More importantly, different MAI ratios influence different dimensions of stability in different ways, although never negatively. Stability is either not influenced by mutualistic interactions -in the cases of population stability and species' spatial distributions- or is positively influenced by them -spatial aggregation, interaction strength-. The question is why do some components of stability are affected by MAI ratio and others do not?

All communities analysed were locally stable, and their stability in terms of the variability in the dynamics of the populations of their constituent species was not affected by the MAI ratio. This could be a consequence of the stabilising effect that space has on complex communities, as has been suggested by others (e.g. [237]), regardless of the types of interactions considered. Several mechanisms that could yield these stability patterns due to spatial arrangements within communities are in place in our model. Meta-community migration, or the exchange of individuals among local populations, could be an important factor determining the fate of species, preventing them from going extinct. Also, the refugee effect created by highly aggregated populations, which prevents predators from attacking individuals at the core of these populations, another mechanisms at place in our simulated communities, could facilitate stability at the population level. As seen in our results, spatial aggregation increases with increasing MAI ratio. This observation, together with the refugee effect we just described could have profound impacts on the ability of predators to capture prey as mutualisms increase.

We showed that the distribution of interaction strengths in the broad ecological network was largely affected by MAI ratios, influencing how stable communities were. The proportion of mutualistic interactions enhances thus the stability of our spatial communities by promoting a reduction in the strengths of the interactions in the ecological network.

Quantitative generality (G_q) is a network-level measure of the generality of consumers in the web of ecological interactions that takes into account the biomass flow through these. In our experiments we observe that increasing MAI ratios results in communities with a lower quantitative generality. This indicates that predators, even when keeping all of their prey species, are becoming more specialised (i.e. they are more likely to interact with some of their prey species than with others). Since our model does not enforce any kind of prey preference or selection, this is exclusively a consequence of an increased abundance of those 'preferred' prey species. A higher proportion of mutualistic interactions promotes thus the dominance of certain prey species that are becoming relatively more abundant. Some of the interactions of generalist species are becoming weaker as a consequence. This could promote a shifting in the distribution of the strengths of interactions towards lower values: a distinctive feature of more stable communities [175, 153].

Another aspect of community stability that we found to be influenced by MAI ratios is spatial aggregation. Both measures of spatial aggregation employed, a global (Moran's I) and a local (Geary's C) one were positively influenced by MAI ratios. This higher spatial aggregation in populations is possibly due to the fact that mutualistic consumers take up fewer resources from their interaction partners when they embark upon an interaction. Populations of mutualistic plants can thus remain more aggregated due to decreased mortality. Regardless of what the mechanisms behind this aggregation at the basal species level may be, this can in turn have similar effects that might ripple up through the food chains in the web as cascading effects, since mutualistic animals would concentrate around their plant prey populations and their consumers will in turn remain aggregated close by them. This might partially explain why interactions in the ecological network are becoming weaker in general, since consumers will be more likely to interact with the same prey species if they are aggregated around them, in detriment of their other potential interactions. Spatial aggregation can have great consequences for reproductive stability, since individuals within more aggregated populations will be more likely to find partners for reproduction (if species reproduce sexually, as it is the case for consumers in our communities). MAI ratios hence positively influence reproductive stability in our spatial communities by promoting greater spatial aggregation as the fraction of mutualistic interactions within the network increases.

As we have seen, the possible mechanisms behind the differential effect of MAI ratios on different aspects of community stability are likely to be related to enhanced spatial aggregation. Larger MAI fractions facilitate the survival, and hence the clustering, of mutualistic basal species and its respective consumers, leaving unaffected the population-level stability of the community (i.e. populations variability is maintained). This phenomenon, at the same time, makes predators to focus exclusively on some of their prey, leaving some of their other prey relatively free of predation pressure. This in turn decreases the interaction strengths of predators vs. the prey it does not encounter so often, effectively shifting the distribution of interaction strengths towards lower values.

Our results seem to contradict those of Mougi and Kondoh [172] who found that high levels of mutualisms have a destabilising effect on the communities with a mixture of antagonistic and mutualistic interactions. Even though, as we have seen, space has an important influence on the stability of natural communities, and that might make the difference between this and previous work, we should not overlook the fact that the results by Mougi and Kondoh were obtained for communities where mutualistic interactions were arranged randomly across the community. In this chapter we tried to approach real communities more closely by choosing to allow mutualistic interactions only between basal (plant) and first consumer (herbivores) species; simulating in this way the phenomenon of plant-animal mutualisms, in which animals are essential for plant reproduction. Also, the 'proportion of mutualistic interactions' in our study refers to the proportion in relation to herbivore links, while in Mougi and Kondohs refers to the whole set of interactions in the community. Thus, MAI ratios of 1 (or 100% mutualism) in this study could correspond to low or intermediate values of mutualism in their study, range in which they found communities to be the most stable. These facts suggest that both studies might actually complement each other.

5.5 Conclusion and future research

For the first time a key component of community assembly that has been linked to stability before: space, is included within a framework of multiple interaction types -a network of networks.

This allows us to extend present theoretical explorations to another type of stability not previously considered: spatial stability. This is key for the understanding of spatial processes such as, for example, the effects of perturbations like habitat loss on community stability. The consideration of space explicitly in models of community ecology has been fundamental to understand questions related to natural phenomena that are not detected in non-spatial or spatially-implicit models, such as percolation thresholds [174, 237]. Our results agree with those obtained by Morales & Vazquez [168] for models of seed dispersal networks and expand these findings to broader networks of different interaction types.

It remains a venue for further research to systematically investigate whether the exact position of mutualistic interactions within ecological networks matter for stability -e.g. randomly distributed versus at the base of the food web-, as it is suggested by looking at our findings in the light of previous ones (e.g. [172]). Even though we have considered spatial ecological communities with a diversity of interaction types, which constitutes a novel approximation to the study of community assembly and stability, we do not investigate particular mechanisms responsible for shaping the networks of interactions in our communities, such as phenotypic and phylogenetic constraints that are behind the existence of 'forbidden links' [187]. An interesting venue for further research would be to develop a more comprehensive study of stability by including into these analyses other dimensions of stability. For example, resilience, measured as the time taken by a community to return to some previous reference state after a perturbation, is a stability metric commonly employed when analysing spatially-implicit models of interaction networks [202]. The present study sheds light on the importance of the diversity of interaction types for ecological communities. Conservation biologists can benefit from understanding how a mixture of interaction types can make ecosystems more stable and by acknowledging the fact that biased losses of certain kinds of interactions from a community can have profound effects on biodiversity and ecosystem stability.

General conclusions

Global change is real. Its effects on biodiversity, community organisation and ecosystem functioning are widespread and profound. A major scientific challenge tackled in this thesis is to delve into the effects of different components of global change on communities and ecosystems. A first step is to address one component of global change at a time before studying their possible synergistic effects, assessing whether different global change drivers have similar consequences on communities. This challenge requires an integrative approach that combines ecological theory, empirical analysis and experimental manipulations. This would allow us to find whether general rules exist regarding the way ecosystems react and will react in the near future to an increasingly human-modified world.

In this thesis I have gone a step further in these investigations by delving deeper into the consequences of several components of global change on food web structure and stability. Additionally, I looked at how different components of stability are related among them in food webs, and how the integration of different interaction types under the same theoretical framework affects our vision of what drives ecosystem stability.

I have employed an integrative theoretical-empirical approach grounded on decades of previous research in ecological complexity and stability, and also on methodologies and concepts derived from research in complex systems, to tackle this problem. I have processed and analysed information from the literature and empirical data to understand how has climatic warming affected multispecies communities. I have contributed to the development of a conceptual framework for the understanding of the relationship between several components of stability and how the former get upset in the face of perturbations like biodiversity loss. Additionally I have developed theoretical models, grounded on ordinary differential equations and individual-based approximations for understanding how complex food webs are affected by biological invasions, and how the mixture of different interaction types within the same ecological network affects community stability, respectively.

This thesis is coincidentally a whole made up of parts, each of which has individually yielded insights that might interact in ‘non-linear’ ways to create an emergent picture of the effects of global change on complex ecological networks; in the same fashion as complex systems, in which the system-level behaviour is much more than the sum of the parts, do. The main emerging conclusions that result from merging the different parts of my thesis are:

1. **Global change increases the uncertainty of the dynamics of novel communities.**

    - I have identified major unknowns in the way novel communities will be re-organised. We still do not know how species are going to interact in these novel ecologies or how strong these new interactions are going to be, because of the mixed evidence that has been found. However, we now have a clearer picture of how this might happen. We are also lacking intuition on how this re-organisation prompted by climate change will affect the dynamics of novel communities; in particular as top-down control emerges as a predominant force in these new ecosystems. We have seen throughout this thesis that the structure and dynamics of novel communities are getting increasingly unpredictable. Our best chance at tackling this problem is by focusing on species traits.

- Another source of uncertainty comes from community stability. How stability is going to be affected by the rapidly changing conditions to which ecosystems are being subject to? We have seen that different dimensions of stability, that were previously correlated, become increasingly uncorrelated after perturbations. Different aspects of perturbations are making communities highly unstable and more fragile to further disturbances.

2. **Non-trophic interactions are important for community stability.**

    - As we have seen, in intertidal and terrestrial communities, interactions other than trophic ones (competition and mutualism, respectively) have the potential of affecting different dimensions of community stability in different ways, effectively influencing correlations between these dimensions. This points to the fact that community stability must be assessed in the light of a comprehensive account of ecological interactions at the community level. This is crucial not only to fully understand, but also to be better able to predict the effects of global change on these communities.
    - Also new measures of community stability, related to the spatial arrangement and distribution of the species in an ecosystem, are affected by different fractions of mutualistic vs. antagonistic interactions. Space is thus an important factor behind community organisation, and the diversity of interaction types is key to fully assess community stability in spatially-explicit settings.

3. **Some features of community organisation and food web structure are similarly affected, while others are affected differently, by different components of global change.**

    - Changes in some characteristics of food web structure, such as network connectivity, are similar for different components of global change, such as climatic warming, species loss or biological invasions, with an increase in connectivity in general. This suggests that species are getting closer to each other, with important implications for the propagation of perturbations across the food web. However, other effects such as changes on the variability of the diet breadth of species within the food web are different when looking at climatic warming (increase) than when looking at biological invasions (decrease), for example. Species traits like diet breadth and body size are thus a fundamental aspect in the understanding of the effects of global change on natural communities.
    - Temporal variability of populations is differently affected by the removal of different species from the same community. Temporal variability of population dynamics measured at the species vs. at the community level is differently affected by biological invasions. Population fluctuations are thus very sensitive to the particular component of global change the community is subject to, making the dynamics of novel communities more uncertain.

The findings summarised above seem to suggest that system predictability would be harder in the face of global change due to further uncertainties and non-linearities. In this thesis I argue that only by embracing uncertainty are we going to be in a better position to predict the effects of global change on ecosystems and the organisation of novel communities. It is time to focus on the search for integrative theoretical-empirical-experimental frameworks that can provide useful insights for predicting the consequences of the biological re-organisation of the planet. We should do this by focusing at the more informative measures of change and ecological stability and at the fundamental processes that play a crucial role in shaping these changes.

Further on-going work

The research developed until now has opened up further research avenues into the study of complex ecological systems, some of which I am currently pursuing. One aspect of global change that can be readily investigated using theoretical models like that presented in *Chapter 5* is habitat loss and fragmentation. I am currently tackling this issue, in collaboration with my supervisor, Dr. Jose M. Montoya, and with Dr. Daniel Montoya, at the University of Bristol, by inducing the loss of parts of the 2D grid in which individuals live. I do this for different fractions of mutualistic interactions within the ecological network. This allows us to assess the importance of mutualisms, and a mixture of interaction types, for the persistence of natural communities in the face of habitat loss.

I am also trying to delve deeper into the relationships between different components of ecological stability. For this I am taking a mixed experimental-theoretical approximation to look at the effects of different kinds of perturbations on community stability in general and the correlation between several types of stability in particular. This work is being developed in collaboration with Dr. Ian Donohue at Trinity College Dublin. We are currently performing manipulation experiments on microcosms made up of several bacterial and protist species with a well-known food web structure. Following an individual-based approximation as the one presented in *Chapter 5*, I am simulating the dynamics of these experiments, this time *in-silico*, in order to perform further experiments that cannot be done *in-vitro* and to provide a theoretical mechanistic explanation for the observed experimental patterns. This approach has the advantage of providing a test bench for our theoretical model using experimental data coming from experiments performed on real ecological communities.

'*Nothing in biology makes sense except in the light of evolution*'. This concise statement, authored by Theodosius Dobzhansky in 1973, and perhaps one of the most famous quotes in biology, strongly advocates to the importance of evolution in any biological setting. I am going further in the investigation of the effects of global change on ecological communities by including evolution into my theoretical framework. Eco-evolutionary dynamics [197] are thought to be one of the fundamental mechanisms behind community organisation and ecological network structure. Because of these, they could form the basis for a proper understanding of the ultimate effects of perturbations on natural communities. I have focused on the incorporation of an evolutionary framework within an ecological setting similar to the one presented in *Chapter 5* for the investigation of the role of eco-volutionary dynamics into community structuring and response to perturbations. This model is being currently particularly tailored for the understanding of the emergence of network structure in complex host-microbe associations between marine sponges and the incredibly diverse bacterial community that live within them. This work is in collaboration with my supervisor, Dr. Jose M. Montoya.

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