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DOCTORADO EN ECOLOGIA TERRESTRE

Structure and Dynamics of Ecological Networks with Multiple Interaction Types

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I am purposely keeping these acknowledgements in the academic side of things. At a personal level, the imprint is even more important, and I could not have carried out this thesis without the love and support of those close to me. Thanks to all of you.

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Abstract

Organisms survive, thrive and reproduce by interacting with individuals of their own and of other species. Biotic interactions are extremely diverse in type, magnitude, or spatiotemporal scale, and give rise to ecological networks with complex topologies and dynamics. Such networks of ecological interactions have been shown to possess non-random structural properties that enhance their resilience and robustness to perturbations, and thus are key elements for understanding the response of species to external forcing such as environmental change or habitat loss.

Despite the importance of interaction networks in studies of ecological communities, and due in part to their sheer variability, ecological interactions are notoriously difficult to document and quantify in a comprehensive fashion. Therefore, historically, studies of ecological networks have focused on the most easily observable types of interactions, those between predators and their prey, or more generally speaking, between consumers and resources. In the last decades, studies of mutualistic networks have also risen to prominence and have demonstrated, for example, that food webs and mutualistic networks have markedly different topologies and this has both ecological and evolutionary consequences for the species involved. One of the main challenges of contemporary community ecology is to expand our understanding of networks of a single interaction type to a more realistic view of ecological communities, by considering how different interactions mutually influence community structure and functioning. In order to tackle this challenge, a first step is to lay down overarching theoretical hypotheses about such complex networks.

In this thesis I approach this general objective and analyse a series of fundamental questions about ecological networks. After a general introduction, first I synthesise current methodologies for developing theoretical network models. I find that three main conceptual approaches have been used, and discuss their relative strengths, weaknesses, and potential uses. Second, I study whether species persistence in model communities is influenced by the frequency and distribution of the different interaction types. The prevalence of positive interactions within a community is shown to be key for species-poor communities, whereas in more speciose communities, different combinations of interactions can occur without affecting species persistence in a significant way. Furthermore, networks with randomly distributed interactions show less species persistence than structured networks. If community structure is important for species persistence, it follows that other community-level patterns should also be affected by it. In the fourth chapter, I focus on Species Abundance Distributions (SADs), one of the most studied patterns in community ecology, and ask whether their shape varies in a consistent way for the different trophic guilds of a community. I compare theoretical expectations with SADs from empirical datasets, and find that SADs of plant communities are significantly less even and more skewed than SADs from mammal ones. Among mammal trophic guilds, there are no significant differences in the evenness or skewness of their SADs. These first chapters deal with the structure and dynamics of closed communities, aiming to establish baseline hypotheses. In the fifth chapter, I incorporate another degree of complexity, namely the spatial perspective. Specifically, I

analyse how interaction effects are propagated in space, such that interactions occurring in a local community may influence other communities connected to it by means of dispersing or foraging individuals. Given the novelty of this analysis and the long tradition of food web models, in this chapter I focus on trophic communities as a simplified model system. I find that the distribution of net effects of a species over another across the metacommunity is significantly different if the local communities are connected by dispersal, foraging, or a mixture of both. In the sixth chapter, I tackle the long-standing question of the variability of species interactions across environmental gradients. For approaching this question, I recover the distinction, originally proposed by G.E. Hutchinson, about scenopoetic and bionomic environmental factors, i.e. non-resource and resource factors. By recognizing that these two types of environmental factors have different effects on species fitness and on the importance of species' pairwise interactions, I analyse the prevalence of positive and negative interactions in model communities across a two-dimensional environmental gradient with one resource and one non-resource factor. I find that, according to the expectations, positive interactions respond to the non-resource factor, whereas negative interactions vary across the two axis of the gradient, with consequences for average persistence time and species diversity across the combined gradient.

Article references

- **Chapter 2:**
  García-Callejas, D., Molowny-Horas, R., & Araújo, M. B. (2018). Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos*, 127, 5-22. doi: 10.1111/oik.04428

- **Chapter 3:**
  García-Callejas, D., Molowny-Horas, R., & Araújo, M. B. The effect of multiple biotic interaction types on species persistence. *Ecology* (in press). doi: 10.1002/ecy.2465

- **Chapter 4:**
  García-Callejas, D. On the variability of Species Abundance Distributions with trophic guild and community structure. Under review in *Global Ecology and Biogeography*

- **Chapter 5:**
  García-Callejas, D., Gravel, D., Molowny-Horas, R., & Araújo, M. B. Manuscript in preparation.

- **Chapter 6:**
  García-Callejas, D., Molowny-Horas, R., & Araújo, M. B. Manuscript in preparation.

N.B.: the code used to generate the results of the different chapters is on the process of being cleaned up, and will be uploaded in its entirety to a public repository, at https://github.com/DavidGarciaCallejas/. As of 20/09/2018, most of the functions related to the model of chapter 3, and the full R code for replicating the results of chapters 4, 5, and 6, are already available. Likewise, the latex files for generating this document are also available. The illustrations for the heading pages of the chapters are all in the public domain, and the authors/name of the works are:

- Introduction: Haboku Sansui, by Sesshū Tōyō

- Chapter 2: El Perro, by Francisco de Goya

- Chapter 3: Street art by El Niño de las Pinturas

- Chapter 4: Street art by El Niño de las Pinturas

- Chapter 5: Crow and the Moon, by Kawanabe Kyōsai

- Chapter 6: Photograph of Cerro Huenes, Granada, taken by the author

- General Discussion: Photograph of a road in Nicaragua, taken by the author

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Introduction

1.1 Community Ecology

Humans have always marveled at the diversity of life forms on Earth. This fascination is reflected in the multitude of ways in which nature is represented and studied in the different branches of human knowledge. Some enjoy looking at the finest detail of the life histories of species and populations. To some of us, life forms are inherently self-organized into larger-scale structures that display their own rules and meaning; thus we look at a forest and see, indeed, a tight entanglement of individuals that cannot possibly thrive without the surrounding web of other species. Individual details, while extremely important, are embebbed into entities that posses their own ecological, aesthetical and etical relevance: ecological communities. While the Clementsian extreme view of communities as full-fledged, delimited entities capable of evolution and reproduction has long been abandoned, it is obvious that associations of individuals do generate predictable sets of processes and patterns, and the main concern of community ecology is with the discovery and understanding of these general processes and patterns. Community ecology is the discipline most directly concerned with the temporal and spatial scales at which individuals interact with each other. Processes intrinsic to this scale are generated by individual-level behaviours, that shape interaction patterns. Whatever the mechanisms by which such community-level patterns are driven, they feedback and influence individual life histories and, in turn, also biogeographic and macroecologic processes, such that the study of community ecology has an important relevance on its own and also plays a key role in understanding the emergence of global patterns from lower-scale processes.

Intuitively, an ecological community can be defined simply as a set of individuals that interact with each other. This broad picture needs to be refined when addressing the systematic study of these entities. For example, how do we define the *set* of species that constitutes a community? What are the *spatial* and *temporal* limits of a given community? In the first chapter of this thesis, for example, we will encounter a community located on a small islet, in which a top predator is a bird of prey that can easily travel dozens of kilometers in a single journey and is thus not constrained by the territory of the islet, whereas other species are sessile or limited to ranges of a few hundreds of meters. Why would I include this top predator as part of the island community, when it clearly has a broader range than the rest of the species? And, looking at this question from another point of view, why would I *not* consider as part of this community other species outside the islet that are also preyed upon by this predator?

The answer, as almost always in ecology, is that no fixed rules are applicable to all cases. Communities, despite their inherent structure and identity, are not organisms with closed physical boundaries to the outside world, and therefore, their spatiotemporal borders are extremely variable and are usually chosen ad-hoc by the investigators studying them. A great deal of studies in community ecology deal with so-called *horizontal* communities. These are simply communities composed of organisms of similar characteristics, usually in terms of taxonomical relatedness. Thus, it is very easy to find studies about the *grassland* communities of a steppe, or about the *arthropod* communities present on the canopy of tropical

trees. Such focus on certain groups of related species is necessary in order to understand in detail certain ecological processes and patterns, such as niche differentiation and coexistence among similar species. It is also very convenient in terms of experimental design, as it allows investigators to concentrate efforts on a small part of the enormous diversity present in every habitat. Studies on horizontal communities are at the core of classic community ecology, and we have learnt much about how species coexist with each other when resources are limited, about how species are positioned along environmental gradients, and about many other ecologically relevant questions.

Notwithstanding the importance and validity of the abstraction of horizontal communities, it is clear that they are somehow incomplete communities, if we recall the broad definition of community sketched above. No one can doubt that, in natural settings, the group of e.g. grassland species is interacting in many ways with other guilds: they are consumed by arthropod or mammal herbivores differentially, they may be pollinated by other sets of species, they may be affected by stamping of big animals or be fertilized by their dung. All in all, communities are more than disjointed taxonomic guilds, and their dynamics are influenced by the whole set of interactions occurring among their constituent species. The role of interspecific interactions is, then, key for understanding and predicting important ecological processes at this scale. It is this vision that has given rise to another long-standing branch of community ecology that has at its core the study of the interactions between different guilds or species within a community: the study of ecological networks. This thesis deals with complex communities represented as networks of interacting species, so I will give a brief overview of network theory in general and applied to ecological communities, and later introduce the specific questions addressed in this thesis.

1.2 Communities as ecological networks

1.2.1 Network theory

Network theory is a branch of applied mathematics that studies the relations between discrete entities, and the emergent properties and structures from these relations. Network theory is generally considered a subset of graph theory, with the main difference between them being that graph theory is more focused on the abstract behaviour of graph classes, whereas network theory is mainly applied to empirical systems and, thus, puts a strong emphasis on the dynamics of the system and its relationship with its structure. The first study that laid the foundation of graph theory is the famous problem of the Seven Bridges of Königsberg formulated and solved negatively by Euler in 1736, and graph theory developed steadily from that initial study. The application of graph theory to complex networks and their dynamics has grown enormously in, specially, the last decades of the 20th century, up to the point that nowadays the study of complex networks is an integral part of a multitude of scientific fields, from social and economic sciences, applied physics or robotics, to virtually every branch of biological sciences. Here I will provide very brief definitions of concepts that will be useful for understanding ecological

networks in general and the investigations of this thesis in particular. It is not my intention to provide a comprehensive introduction to network theory (the reader is referred to Newman (2010) and Barabási and Pósfai (2016) for overviews on that general topic), but rather to review the basics from which ecological networks can be understood and analyzed.

Starting with the building blocks of networks, we may define a **graph** as a pair of sets $G = (V, E)$, where $V = \{v_1, v_2, ..., v_n\}$ is the set of **nodes** of the graph, and E is the set of **edges**, or links, of the graph connecting pairs of nodes. The set E can be any subset of all ordered pairs of V, such that $E \in V \otimes V$. Graphs can be either **directed** or **undirected** depeding on whether their constituent links are directional, i.e. whether $[v_i, v_j] \in E$ implies $[v_j, v_i] \in E$ (Fig. 1.1). Further, simple graphs are antirreflexive, meaning that a node cannot be linked to itself, i.e. $[v_i, v_j] \in E$ implies $i \neq j$.

Such a simple configuration can be easily extended by considering weighted or quantitative links. By incorporating weights, a **weighted graph** is a quadruple $G = (V, E, W, f)$, where V and E are the sets of nodes and edges defined above, $W = \{w_1, w_2, ..., w_n\}$ is a set of weights such that $w_i \in \mathbb{R}$, and $f : E \to W$ is a mapping assigning weights to edges.

Intuitively, we say that two nodes v_i and v_j are **adjacent** to each other, or connected, if they are joined by an edge $e = \{v_i, v_j\}$. Similarly, two edges are adjacent if they are incident to at least one node.

The most basic structural property of a node is its **degree**. It is defined simply as the number of links incident to it. In directed graphs, one may distinguish in-degree, the number of links incident to a node, from out-degree, the number of links incident from it.
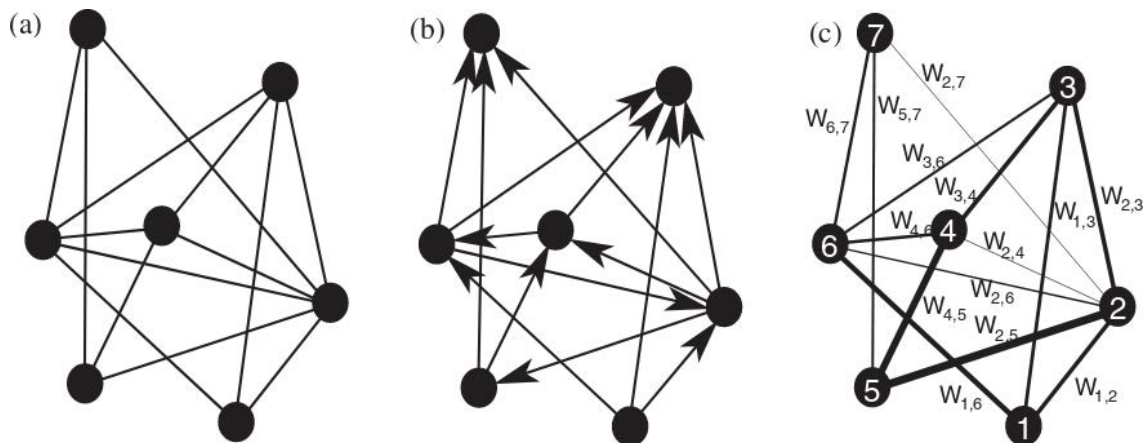
FIGURE 1.1: An undirected (a), a directed (b), and a weighted undirected (c) graph. From Boccaletti et al. (2006)

The **shortest path** connecting two nodes v_i and v_j is defined as the path with the shortest number of edges that connects them. This quantity, L_{min}, is also called the **distance** between two nodes. For weighted graphs, this definition may be refined to consider edge weight, such that the shortest path is the one that minimizes the summed weight of the edges connecting the two nodes.

A graph, in the context of network theory, is termed a **network**, and we will use this term hereafter. A network is said to be **complex** when it possesses topological features that are neither random nor completely regular. These features refer to properties of the network as a whole, and three of the most widely studied features of network are their degree distribution, their average path length and their clustering coefficient.

The **degree distribution** of a network is the probability distribution of the degrees of the network nodes. It is an important property of complex networks, as the degree distributions of random networks differs systematically from that of empirical networks of different types (Barabási and Albert, 1999). While randomly assembled networks display Poisson degree distributions, many real networks are best represented as having power-law degree distributions. This means that in real networks, most nodes are typically connected to only a few other nodes (i.e. have a low degree), whereas a small number of nodes are highly connected. Networks with power-law degree distributions are alternatively called **scale-free networks** (Fig. 1.2).

The **average path length** of a network is the average of the shortest paths between each pair of network nodes. It is given by

$$L = \frac{1}{S(S-1)} \sum_{i,j=1,S; i \neq j} L_{min}(i,j) \tag{1.1}$$

and gives a measure of connectedness between any pair of nodes. Both random and scale-free networks display characteristically short average path lengths (Montoya and Solé, 2002).

Another important topological property is the **clustering coefficient**. It measures the degree to which the neighbours of a given node are linked together. Given a node i with degree d_i, its local clustering coefficient is defined as

$$C_v(i) = \frac{2E_i}{k_i(k_i-1)} \tag{1.2}$$

where E_i is the number of links between the k_i neighbors of node i. The clustering coefficient of the network is the average over all S nodes:

$$C_v = \frac{1}{S} \sum_{i=1}^{S} c_v(i) \tag{1.3}$$

When considering network topology, networks without any differentiation between nodes, where each node can in principle interact with any other node, are called **unipartite**. Another common type of ecological networks is that which represents two disjoint groups that interact with each other but not with members of the same group (for example, a network with a group of plant species and a separate group of pollinators, Fig. 1.3). Such networks are called **bipartite**.

Several other network properties are widely used in the context of ecological networks. Here I will mention three of them. First, the **connectance** of a network
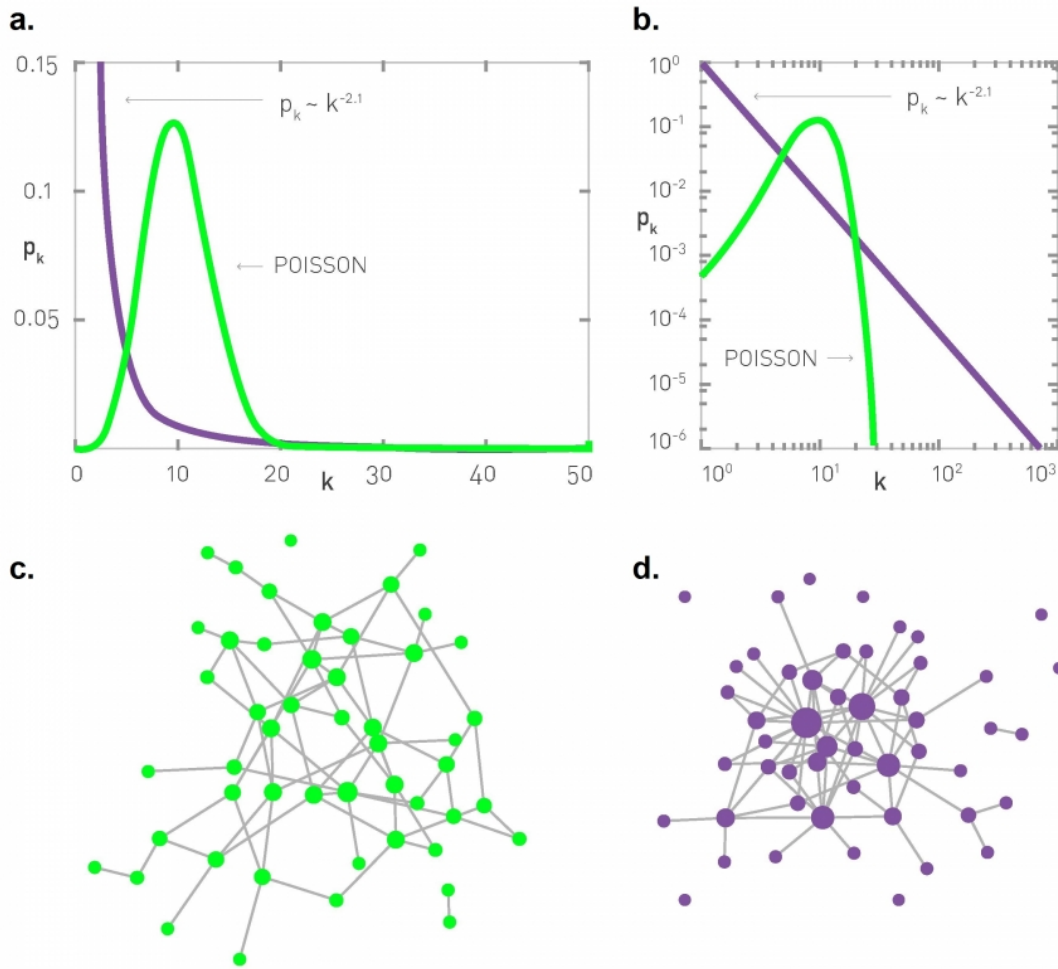
Figure 1.2: Degree distributions from random (green) and scale-free networks (purple) in natural (a) and logarithmic (b) axes. The hubs present in scale-free networks are evident in the network depiction (d). From Barabási and Pósfai (2016)

is the proportion of realized links with respect to the potential number of links in the network. It is defined in different ways depending on the assumptions about the feasible links of the network. Four variations are possible regarding the directedness of the network and the feasibility of self-loops. The most general case is a directed network where self-loops are allowed. In that case, the set of potential links is simply $L_p = S^2$ for a network of S nodes. If self-loops are not allowed, the set of potential links is $L_p = S^2 - S$, whereas if the network is undirected, the number of potential links halves, i.e. $L_p = S^2/2$. Therefore, an undirected network with no self-loops has $L_p = (S^2 - S)/2$ potential links. The general definition of connectance is

$$C = \frac{L}{L_p} \tag{1.4}$$
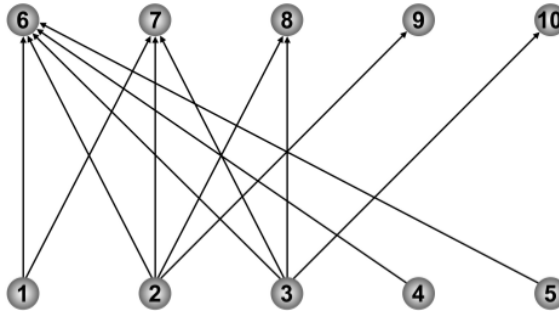
FIGURE 1.3: A bipartite network, in which nodes 1-5 and nodes 6-10 form sets that do not have within-group links. The network is also nested: the diet of consumer 8 is a subset of that of consumer 7, which in turn is a subset of that of consumer 6. From Ings et al. (2009)

where L is the number of realized links.

The above definitions of the set of potential links imply that, aside from the consideration of self-loops, all links between any pair of species are potentially feasible.

Another topological property widely studied, **modularity** is the tendency of the network to display modules highly connected within but largely disconnected from each other. The detection of modules, or clusters, in networks is an active area of research, and a closed definition of modularity depends on the expected number of modules and their link distribution. As an example, Fortuna et al. (2010) defined modularity as

$$M = \sum_{s=1}^{N_M} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right] \tag{1.5}$$

Lastly, **nestedness** is a property of bipartite networks by which nodes with low degree are connected to a subset of the nodes linked by nodes with high degree (Fig. 1.3).

Aside from these general definitions, it is important to mention the matrix representation of networks. Intuitively, by defining a matrix A of dimensions $S * S$, its entries $a_{i,j}$ may represent the existence (or weight) of a link between nodes i and j. Such matrix is called the **adjacency matrix**. If the network is undirected, its adjacency matrix is symmetric, i.e. $a_{i,j} = a_{j,i}$

$$A_{undirected} = \begin{pmatrix} 0 & 1 & 0 \\ 1 & 0 & 1 \\ 0 & 1 & 0 \end{pmatrix}$$

where $a_{i,j} = 1$ if a link exists between nodes i and j, and $a_{i,j} = 0$ otherwise. If the network is directed, the possibility exists that $a_{i,j} \neq a_{j,i}$, so that an example matrix can be

$$A_{directed} = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 0 \\ 1 & 1 & 0 \end{pmatrix}$$

The convention for directed networks is that adjacency matrices represent the interaction originating in column j and affecting row i, so that in the previous example, there is a link from node 2 to node 1, but not the other way around.

1.2.2 Ecological networks: brief history, recent developments and open questions

The general definitions outlined above can be applied to ecological systems seamlessly by defining individuals, species or guilds as nodes, and the biotic interactions among them as the edges or links connecting them. Indeed, natural historians and early ecologists had recognized the network nature of ecological communities long before the recent developments on complex networks. The brief historical review that follows draws primarily from the works by Bersier (2007) and Ings and Hawes (2018), and the reader is referred to these studies for consulting primary references.

The first documented observations about the interactions of species can be traced back to Ancient Greece, where mutualistic relationships were observed by Herodotus, Theophrastus and Aristotle. In turn, the arab scholar Al-Jahiz is believed to have introduced the concept of food chain in his *Book of the Animals*, in the 9th-century. In the early Enlightenment the documented study of the natural world began to gain back attention, although admittedly on a secondary position with respect to mathematics, physics, chemistry or astronomy, disciplines that constituted the main focus of the Scientific Revolution. Observations about empirical food chains are documented by van Leeuwenhoek and Linnaeus, but it would be Alexander von Humboldt in the 19th-century, throughout all his works, the first and most influential proponent of a view of nature that emphasized the complex web of relationships between species, looking at nature as a "living whole". The first representation of a full network of trophic interactions dates from 1880, and was made by the italian scientist Lorenzo Camerano.

After these and other seminal contributions, the 20th-century saw the confirmation of network-oriented approaches to ecological issues. The ecologist Charles Elton developed many important concepts, such as the "pyramid of numbers" by which abundances decreased along the food chain, and established the terms *food chain* and *food cycle*. After his seminal works, the network representation of trophic relationships became a common framework for studying ecological communities. By this point, trophic relationships were already the most studied interactions in ecological communities. Trophic interactions are ubiquitous in nature, they are usually the easiest to document and, unlike other interactions, can be used to outline the fluxes of biomass and energy in a given community. It is, therefore, not surprising that they took, and still maintain, such a predominant role in studies of ecological networks. The figure of Raymond Lindeman also stands out in the first half of the 20th century, with his work "The trophic dynamic aspect of ecology", in which he studied for the first time the quantitative fluxes and feedbacks between the biotic and abiotic components of an entire ecosystem, the Cedar Bog Lake in Minnesota (Lindeman, 1942). As Ings and Hawes (2018) note, limnology had a prominent position on these early developments, and many

temperate lakes were the first ecosystems to be thoroughly sampled and studied.

In parallel to these insights from natural systems, the mathematical foundations for studying the dynamics of ecological interactions were being developed. The mathematician Alfred J. Lotka proposed in 1920 a set of equations for the population dynamics of a pair of predator and prey species, that explained the apparent oscillations observed in plant-herbivore systems (Lotka, 1920). In an independent contribution another mathematician, Vito Volterra, derived similar equations following observations of fish catches in the Adriatic Sea (Volterra, 1928). The general form of these equations is

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y \tag{1.6}$$

where x is the number of prey, y is the number of predators, α is the growth rate of the prey, β the predation rate coefficient, δ the predator's growth rate, and γ its mortality rate. In this model, both species modulate their abundances in response to the other (Fig. 1.4), and the non-trivial solution to the system, formulated as with eq. 1.6 is stable and periodic. The Lotka-Volterra set of equations implies a series of assumptions about the underlying biological system. First, they are an example of a mean-field system, thus assuming an homogeneous habitat in which individuals are interacting without constraints or variations. Prey populations in the absence of the predator display exponential growth (i.e., if $y = 0$, the variation in prey density is given by αx), and the predator depends entirely on the prey population. Furthermore, predators do not satiate, in that they respond instantaneously to increases in prey population. Importantly, all $\alpha, \beta, \delta, \gamma$ coefficients are constant, thus assuming no other sources of variation.
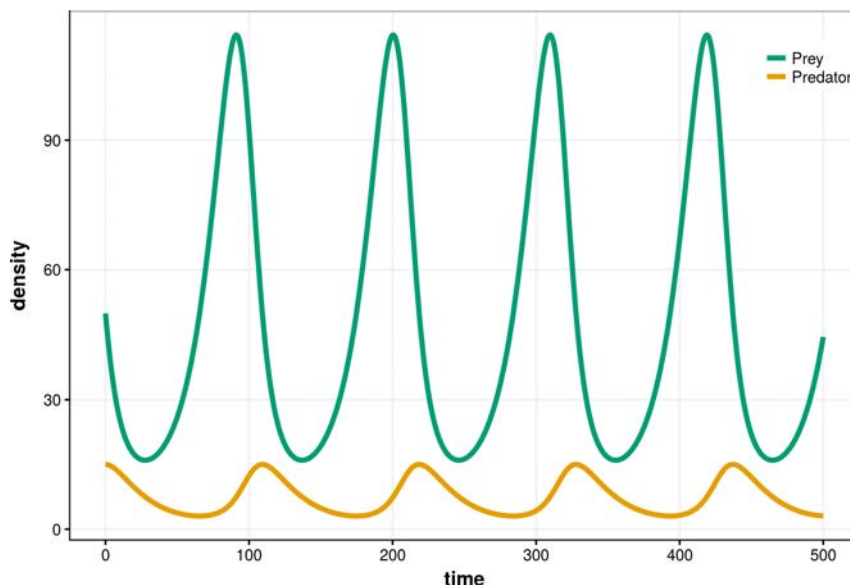
FIGURE 1.4: Lotka-Volterra equations generate stable population dynamics in which densities of the prey and the predator species are both dependent on each other.

In the context of dynamical systems, the stability of the system can be approached by analysing how the system responds to very small perturbations off

a steady state. This is done by calculating the *eigenvalues* of the system, values that encapsulate the response of the system to such a small perturbation around the equilibrium. The mathematics behind the calculation and interpretation of eigenvalues have been thoroughly developed, and the interested reader may find innumerable derivations of it. In the context of ecological networks, the book *Food Webs* by Kevin McCann (2011) gives a well-balanced introduction to the study of dynamical systems. The important message is that the eigenvalues of a dynamical system (in particular, the maximum eigenvalue) are informative about the stability of the system. Positive eigenvalues will imply that the system is locally unstable, whereas negative eigenvalues mean that the system is locally stable around that particular equilibrium.

Despite the initial insights from 2-species model systems, many ecologists were, as we have seen, much more interested on the notion of stability of whole communities or ecosystems. The first conceptual treatments of community stability can be traced back to Eugene Odum, who suggested that in a community, the number of alternative paths a quantum of energy has for going from primary producers to top predators is a measure of the stability of the community. This notion that the more links an ecological network had, the more stable it was (or, in other words, that "complexity begets stability"), was the prevalent opinion up until the early 70s. Robert MacArthur, in another highly influential study, analyzed the stability of complete food webs in a semi-quantitative way. He arrived to the hypothesis that community stability increases by either increasing the number of species in a community, or the connectance of the associated food web (MacArthur, 1955).

The complexity-stability dichotomy of ecological communities entered a new dimension after the seminal work of Robert May (May, 1972), who used for the first time mathematical models of idealized communities to assess the local stability of systems with an indeterminate number of species modelled with Lotka-Volterra dynamics. He found that, in randomly assembled networks with normally distributed interaction strengths, the dynamical systems remain locally stable if

$$\alpha \sqrt{SC} < 1 \tag{1.7}$$

where α is the average interaction strength, S is the number of species, and C is the connectance of the network in the form L/S^2. The interpretation is that an increase in either mean interaction strength of the system, species richness, or number of links, would rapidly tend to destabilize the system. Crucially, May was of course aware of the limitations of his approach: the assembled networks possessed no structure whatsoever, pairwise interaction strength was assumed to be a constant, stochastic parameter, and the definition of stability involved infinitesimally small perturbations from an equilibrium state, as given by the eigenvalues of the system. Nevertheless, regardless such obvious limitations, May's work was the first quantitative derivation about the expected stability of arbitrarily large ecological communities, and not only so, but it also was a frontal attack on the common wisdom championed by MacArthur (who passed away way too early, in 1972) and many others by that time. The debates and

number of studies triggered by May's results are countless, both in the camps of the theoreticians and the empiricists. From that moment onwards, the study of ecological networks started to gain even more attention and took many different parallel paths. An important line of research, that did not start with May's results but definitely gained attention after them, follows the estimation of interaction strengths both in theoretical studies of functional responses (Holling, 1965) and empirical estimations (Bender et al., 1984).

Robert Paine showed in 1966 that the effects of removing a top predator could propagate throughout the whole ecological network, eventually altering the richness of the community (Paine, 1966). This striking result led to the denomination of *keystone species* to those species with a disproportionate influence in the overall structure and dynamics of the community. He continued to be interested in measuring the impacts of one species over another and on the overall community, a theme that came together with the theoretical importance of interaction strength proposed by May. Theoretical metrics of interaction strength represent changes in different per capita or population-level parameters (Laska and Wootton, 1998) but such metrics are, importantly, not generally equivalent to what is measured in experimental studies (e.g. Bender et al. 1984). Paine observed that descriptions of food webs that failed to account for estimates of interaction strengths were not enough in order to link the structure of food webs with their dynamical behaviour (Paine, 1992).

However, obtaining empirical estimates of all interaction strengths in a given network is so far unfeasible even for moderately rich communities, given the complexity of the combinations and feedbacks of effects between the different species involved. This divide between theoretical models and empirical estimates of interaction strengths is still one of the main unresolved problems in network ecology. Theoretically, it has been shown that, within the framework of local stability analyses and for networks considering only trophic interactions, stability is enhanced when a majority of interactions are comparatively weak and only a few are comparatively strong (McCann et al., 1998; Berlow, 1999). Incidentally, a recent article showed this pattern to hold in a set of empirical food webs (Jacquet et al., 2016).

Aside from the studies on theoretical and empirical interaction strength, and its importance on community stability, another strong source of discussion arising from May's results is the role that non-random structural patterns played in conferring stability to empirical networks. The first empirical food webs to be collected and analysed for structural regularities approach in the late 70s, in particular in a seminal book by Joel Cohen (1978). An early focus of studies on food web structure was the role of *connectance*, given its relationship to theoretical stability (eqn. 1.7). Early efforts tested, for example, the potential invariance of the relationship between number of links and number of species L/S, as a means of corroborating May's criterion (see Pascual and Dunne 2006 for details).

The early compilations of empirical food webs, however, were not even close to be complete descriptions of their systems, and had important flaws such as differential level of node taxonomic aggregation. Newly collected data in the early 1990s (Polis, 1991; Martinez, 1991) showed that network metrics and relationships outlined with earlier food webs were in many cases artifacts of the poorly collected

data (Pascual and Dunne, 2006), and this realisation triggered a reorientation of efforts and development of new hypotheses and ideas concerning food web structure. Among them, an important theoretical model of food web structure, the niche model (Williams and Martinez, 2000), proved able to generate food webs with realistic structural patterns out of a single niche axis in which all consumer species are sorted. More recently, species-level traits and their distribution have proven to be important in characterizing food web structure, as shown for example by Laigle et al. (2018).

In parallel to these more recent developments on food webs, studies on other types of interactions started to emerge in the late 20th century. The first attempt at characterizing a network of positive interactions was made by Pedro Jordano (1987), who studied patterns of connectance and interaction strength in plant-pollinator and plant-seed disperser networks. From his seminal study, a whole field of research opened up, and the study of bipartite mutualistic networks has produced many insights regarding the structure and dynamics of these communities (Vázquez et al., 2009; Bascompte and Jordano, 2013). In particular, bipartite mutualistic networks have been shown to be generally nested, and this nestedness is an important feature for their stability, as opposed to food webs, which are thought to be comparatively less nested and more modular (Thébault and Fontaine, 2010).

It is now sufficiently clear that, in any case, mutualistic interactions are structured in a non-random fashion in empirical bipartite networks, and this structure has important consequences for their dynamics. Regarding the study of interaction strengths in mutualistic networks, the functional responses of mutualism are much less studied than those of predator-prey interactions (Holland et al., 2002), and a novel line of research focused on estimating the net impact of a species over another by using as a surrogate their interaction frequency (Vázquez et al., 2005). This approximation is likely dependent on the specific type of mutualism considered. For example, in a study analysing plant-hummingbird networks, Vizentin-Bugoni et al. (2014) showed that trait-matching was more important for structuring these ecological networks than abundances alone. In further studies, interaction frequency itself has been found to be well approximated by the abundances of the interacting species (Vázquez et al., 2007). This methodology for estimating population-level short-term impacts is thus promising for mutualistic networks in which no other quantitative effects are available. Importantly, the approximation hinges on interactions being stochastic, with no trait-mediated selection of interaction partner or frequency. In that sense, it may also serve as a baseline against which to compare the effect of traits in specifying interactions (Poisot et al., 2015).

All in all, the knowledge about the structure and dynamics of single-interaction ecological networks has increased enormously in the last few decades. A fundamental question that we may ask is the extent to which these varied insights are applicable to empirical, complex communities. Despite the convenient distinction between interaction types commonly made for studying ecological networks, communities are composed of individuals interacting in many different ways, with varying intensities and at different spatial and temporal scales.

We know now that, at the very least, both predator-prey and mutualistic in-

teractions are highly structured in empirical communities. We lack, however, a general framework for ecological networks in which different interaction types are integrated, and where the combined structure of the network can be analysed. This integration, of course, will have important implications for community dynamics: for example, including non-trophic interactions onto food webs has already been shown to importantly alter their stability patterns (Kéfi et al., 2012, 2016), or their robustness to secondary extinctions (Pocock et al., 2012). This change of scope about ecological communities may also trigger novel questions about their structure and dynamics. It may seem surprising on a first look, but we currently do not know how the different interaction types are distributed in empirical communities generally. Actually, given the difficulty of compiling different interaction types in a systematic way for any relatively rich community, it becomes clear that approaching such a fundamental question requires important observational and experimental efforts. In that sense, a general theoretical framework for multiple interactions networks may help develop targeted hypothesis about empirical communities, from which to build observational or experimental studies. Related important questions concern the role of spatial patterns or environmental gradients in shaping the combined structure of ecological networks. For example, does the spatial structure of the different interaction types vary? How does this influence the spatial propagation of effects? Does the relative importance of the different interaction types vary across environmental gradients?

In single-interaction networks, the role of space in shaping their structure and stability has been recognised as a key factor, e.g. by analysing how different communities are connected by dispersal and the implications for the overall metacommunity (Leibold et al., 2004), or how network structure varies with spatial scale (Galiana et al., 2018).

In order to integrate recent advances on multiple interactions networks with the spatially explicit framework of metacommunity ecology, some issues need to be resolved before a proper multiple interaction metacommunity framework is developed. For example, what is the nature of the connections between spatially separated communities? Mobile species are capable of displacements in order to look for food sources (antagonism, mutualism), or in order to establish themselves in another territory (dispersal). It is important to know if there is a relationship between the movement capacity of a given species and its tendency to engage in different interaction types. It is also important to develop theory on the spatial propagation of interaction effects: how do the different types of interaction propagate in space? Are some interaction types more likely to have a greater impact on the overall community than others? Or is the effect only related to the relative magnitude of the interaction, and the centrality of the species involved?

Some of these questions have been barely explored even in metacommunities of single interaction types. Most metacommunity studies follow the long-standing history of horizontal communities and consider how competitive guilds are connected in space, and only recently is metacommunity theory being expanded to account for mulitrophic networks (McCann et al., 2005; Fahimipour and Hein, 2014; Gravel et al., 2016b). It is therefore necessary to strenghten the foundations of metacommunity theory before integrating it with the paradigm of multiple interactions networks.

From a more general point of view, one can also ask whether the structure and dynamics of ecological networks vary across different types of gradients, and if so, what are the factors and processes driving this variability. The variability of ecological interactions across environmental gradients has been studied under different subfields of community ecology, from the point of view of horizontal communities (mainly plants: the Stress Gradient Theory, see e.g. Maestre et al. 2009) and theoretical food webs with competitive interactions (Environmental Stress Models, see Menge and Sutherland 1987). Stress Gradient Theory focuses on evaluating the response of communities to variations in environmental stress, and does so by studying plant communities which, as stated by theory and empirical observations, may exhibit variations in the relative importance of competitive versus facilitative interactions as stress increases (Callaway and Walker, 1997). This theory, however, is currently not applicable to multitrophic communities, despite recent attempts to test its validity for higher trophic levels (Barrio et al., 2013). Environmental Stress Models, in turn, were developed to predict the differential role of top-down and bottom-up processes in food webs across gradients of environmental stress. While theoretically comprehensive, their difficulty of testing has prevented further developments except for localised, targeted systems (e.g. Cheng and Grosholz 2016; Daleo et al. 2015). In any case, none of these theories incorporates the whole array of interactions potentially occurring in nature, and a further issue is that the different types of environmental gradient that mediate ecological processes are usually taken together, without differentiating the different environmental components that may affect interactions and demographic processes. Therefore, we are still far from a general theory on ecological networks and their variability across environmental gradients.

1.3   Objectives

In my thesis I addressed fundamental unresolved questions about ecological networks in general. Chapters 2 and 3 deal explicitly with networks of multiple interaction types, and the rest of the thesis explores fundamental questions for which more simple model systems are used, in order to focus on the specific questions at hand before adding the complexity of multiple interactions. The following general objectives constitute the main chapters of the thesis:

- **To review and synthethise current methodologies for modelling multiple interactions in ecology**

  First, I aimed to synthesize and organize the growing literature on this type of networks, while at the same time laying down some methodological foundations for future theoretical studies on the subject.

- **To understand how the frequency and distribution of the different interactions drive species persistence**

  Second, I developed a general theoretical model in which I tackle several

key issues about network structure and dynamics. I aimed at deriving general hypotheses about the persistence of species in complex networks with realistic structural patterns.

• **To know how Species Abundance Distributions are influenced by the structure of multitrophic communities**

Third, I looked at a classic pattern from horizontal community ecology, the Species Abundance Distribution, from a network perspective. In order to understand how the frequency and/or distribution of interaction types influences the distribution of abundances in a given community, first it is necessary to develop theoretical expectations about its distribution on more simple networks, for example food webs. I drew from the extensive literature on food webs and trophic relationships in general to derive basic hypothesis about the variation of Species Abundance Distributions across trophic guilds.

• **To advance in the understanding of interaction effects in space**

Fourth, I studied the role of space in propagating interaction effects. As with the previous chapters, no general hypotheses exist about the spatial propagation of interaction impacts, so in order to provide baseline expectations and for our study to be comparable to previous efforts, I focused on the effect of trophic interactions and how they propagate when species disperse or forage in a set of spatially connected communities.

• **To explore whether environmental factors drive the frequency of different types of interactions**

Fifth, I studied how interactions are likely to vary across environmental gradients. This issue has been explored independently in different subfields of community ecology, but the conclusions obtained have been largely overlooked in other fields. I recovered the classic differentiation in environmental factors first proposed by Hutchinson and delve in how gradients in different types of environmental factors may drive variations in the prevalence of different interaction types and other community properties. Given the paucity of studies and theory in this question, I took the same approximation as in chapters four and five, and resorted to basic horizontal communities, in order to provide general foundations from which ideas about more complex communities can be developed.

Multiple interactions networks: towards more realistic descriptions of the web of life 2

Abstract

Ecological communities are defined by species interacting dynamically in a given location at a given time, and can be conveniently represented as networks of interactions. Pairwise interactions can be ascribed to one of five main types, depending on their outcome for the species involved: amensalism, antagonism (including predation, parasitism and disease), commensalism, competition or mutualism. While most studies have dealt so far with networks involving one single type of interaction at a time, often focusing on a specific clade and/or guild, recent studies are being developed that consider networks with more than one interaction type and across several levels of biological organisation. We review these developments and suggest that three main frameworks are in use to investigate the properties of multiple interactions networks: 'expanded food-webs', 'multilayer networks' and 'equal footing networks'. They differ on how interactions are classified and implemented in mathematical models, and on whether the effect of different interaction types is expressed in the same units. We analyse the mathematical and ecological assumptions of these three approaches, and identify some of the questions that can be addressed with each one of them. Since the overwhelming majority of studies on multiple interactions are theoretical and use artificially generated data, we also provide recommendations for the incorporation of field data in such studies.

2.1 Community ecology and network theory

Ecological communities should be defined not only by lists of co-occurring species, but also by the myriad of interactions taking place among them. A convenient way to include information about both species composition and their interactions is to represent communities as networks in which species are nodes connected by links representing biotic interactions. Network analyses can provide insights into community local stability (Allesina and Tang, 2012) and robustness to extinctions (Riede et al., 2011), the degree of specialization of individual species or guilds (Dorado et al., 2011), the impact of invasive species or climate change on established communities (Lopezaraiza-Mikel et al., 2007) and, more generally, on any question in which pairwise interactions relate to community patterns and processes.

Networks can accommodate different types of data, depending on the nature of the links between species (e.g., qualitative, quantitative, static, dynamic), the temporal and spatial resolution of the community, the level of aggregation of the nodes (e.g., individuals, species, trophic guilds), or the specific objectives of the study. A common simplification is to study networks of a single interaction type, e.g., trophic (McCann, 2011) or mutualistic (Bascompte and Jordano, 2013), assuming (often implicitly) that the effect of other interactions on community dynamics is negligible compared to the ones analysed. Such an assumption is usually unavoidable given the lack of comparable data on different interaction types, but it is becoming increasingly clear that the effects of interactions not accounted for in analyses of single-interaction networks (including indirect ones; but see Cazelles

et al. 2016) might be significant for species persistence (Soliveres et al., 2015; Kéfi et al., 2016) and community structure (Sander et al., 2015; Golubski et al., 2016). Furthermore, analyses of interaction networks of a single type often yield differential results regarding the factors that drive their stability. For example, among the factors reported to stabilize food webs are high modularity and low connectance (Thébault and Fontaine, 2010), correlation in pairwise interaction strengths (Tang et al., 2014), trophic coherence (Johnson et al., 2014), a preponderance of weak (McCann et al., 1998) and asymmetrical interactions (Bascompte et al., 2006), degree distributions broader than those of random graphs (Allesina et al., 2015), or the appearance of generalist consumers coupling resources with different interaction strengths (Rip et al., 2010). On the other hand, mutualistic networks are thought to be more stable when highly nested and connected (Thébault and Fontaine, 2010; Lever et al., 2014), when there are demographic responses to interactions (Lee, 2015), or when mutualistic interactions are relatively strong (Rohr et al., 2014). The persistence and resilience of communities defined with multiple interaction types, however, will additionally likely be influenced at least by (1) the proportion of the different interaction types, (2) the relative strength of pairwise interactions both within and among interaction types, and (3) the structural properties of each sub-network and the overall aggregated network.

The study of single-interaction networks in ecology has progressed enormously in the last decades, both theoretically and empirically. In parallel, the analysis of multiple interactions networks has also advanced in other fields of study (Boccaletti et al., 2014). This novel paradigm has only recently started to be applied to ecological studies, with several examples of new conceptual developments being forged together with applications of old concepts to new problems (Table 2.1). Despite the relatively small number of studies using multiple interactions networks in ecology, the research objectives and methodologies that have been addressed are extremely diverse, and a synthesis of recent developments is timely. Here, we identify three main approaches for the design and analysis of ecological multiple interactions networks. These approaches have been used in theoretical and empirical studies without an explicit recognition of their conceptual underpinnings. We define them explicitly, examine their underlying ecological assumptions, the type of questions best addressed with each approach, and provide recommendations for the integration of empirical data.

2.2 Multiple interactions networks in ecology

Probably, the first study of ecological networks explicitly considering different interaction types was the classic study by May (1972), in which he assembled interaction matrices with random coefficients from a Gaussian distribution $N \sim (0, \sigma)$, thereby allowing for negative and positive pairwise interactions to be considered. May's results showed that in theoretical communities assembled randomly, complexity (measured as connectance and species richness) was inversely related to the local stability of the system. But natural communities are highly complex, diverse and, nonetheless, seem to persist. After that seminal study, there has been a flurry of studies trying to uncover the processes and structural patterns that

confer stability to empirical communities (e.g. Saint-Béat et al. 2015). However, comparable data on different interaction types is extremely difficult to acquire, and the focus for most of the second half of the 20th century has been on how competitive and antagonistic interactions drive population and community patterns (e.g. Connell 1961; Paine 1966). As predator-prey interactions are easiest to observe and document in the field, the analysis of empirical networks relied almost entirely on food webs for a few decades. Pioneering works by Jordano (1987), or Fonseca and Ganade (1996), amongst others, paved the way for the study of mutualistic networks, but the first studies considering more than one interaction type in the same network only appeared in the last decade (Table 2.1).

Developing a theoretical framework for multiple interactions networks involves the integration of a variety of interaction types and effects, direct and indirect, taking place at different temporal and spatial scales. In this review, we propose two main criteria for classifying such frameworks. The first is the classification system applied to interactions (Abrams, 1987). Interactions can be defined based on the effect they produce on each member or, alternatively, on the mechanism by which the interaction is produced. Regarding effects, each interactor can be affected positively, negatively, or not affected at all by a pairwise interaction, regardless of the actual mechanisms by which the effect occurs. For example, a (-,-) interaction, defined as competition, could actually be realized through mechanisms as different as territorial, chemical or consumptive competition (Schoener, 1983). By defining all interactions with respect to the effect on each member (0,-,+), every effect-based classification is complete, in the sense that no interaction, however idiosyncratic, is left unclassified. Regarding mechanisms, interactions are defined according to the mechanism by which they take place, regardless of the effect on the interacting species. Thus, consumptive competition would be defined as an interaction in which each member is affected by consumption of a common limited set of resources, territorial competition would represent limitations on the available space for each interactor, and so on. A virtually unlimited number of interaction categories can be theoretically defined under this scheme, depending on the questions addressed.

The second criterion distinguishes network analyses based on whether the strengths of different interaction types have common units (i.e., their effects are comparable, acting upon the same population property) or not. This criterion only applies to classification schemes based on effects as, by definition, strengths of interactions acting explicitly through different mechanisms have different units, and are thus not amenable to being homogenized. For example, chemical competition between two plant species may be reflected on the mortality rates of the interacting populations, while a mutualistic interaction between a plant species and a seed disperser bird may affect the dispersal rate of the plant and the population growth rate of the bird. In an effect-based classification with the same units for every interaction, on the contrary, these and every other interaction could be taken to affect a single property (e.g. long-term population size), and hence would be comparable. Based on the two criteria proposed here, we distinguish three conceptual frameworks, already found in the literature, to construct and analyse multiple interactions networks: expanded food webs, multilayer networks, and equal footing networks (Fig. 2.1).

Table 2.1: Studies considering networks of more than one interaction type. Analyses of small network modules (<5 species) are not included

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Arditi et al. 2005	Expanded food web	Mechanism-based	+ and – modifications to trophic interactions	Model coefficient	Synthetic	Communities with positive non-trophic interactions tend to incorporate almost all available nutrients
Lafferty et al. 2006	Expanded food web	Mechanism-based	Predator-prey and several parasitic interactions	Binary	Empirical data from four food webs containing parasites	Links involving parasites are a majority in food webs, and their inclusion modifies structural metrics
Goudard and Loreau 2008	Expanded food web	Mechanism-based	+ and – modifications to trophic interactions	Model coefficient	Synthetic	Interaction webs that include trophic and non-trophic interactions are expected to have a lower local richness, biomass, and production than food webs that include only trophic interactions
Lafferty et al. 2008	Expanded food web	Mechanism-based	Predator-prey and several parasitic interactions	N.A.	N.A.	Lines of research to integrate parasitic interactions into food webs
Kéfi et al. 2012	Expanded food web	Mechanism-based	N.A.	N.A.	N.A.	Conceptual framework for including non-trophic interactions in food web studies.

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Donadi et al. 2013	Expanded food web	Mechanism-based	Effects of allogenic ecosystem engineers	Measurements of clorophyll content in sediment	Empirical experiment	Facilitation of ecosystem-engineering cockles in benthic primary producers on intertidal flats
Majdi et al. 2014	Expanded food web	Mechanism-based	Effects of predators (flatworms) on litter decomposition and community assembly	Carbon content in leafs, biomass of different guilds, sediment content	Empirical experiment	Flatworms have significant effects on the variables measured, overriding direct trophic effects
Sanders et al. 2014	Expanded food web	Mechanism-based	Different effects of ecosystem engineers	N.A.	N.A.	Integration of ecosystem engineering effects into food web analyses
Bachelot et al. 2015	Expanded food web	Mechanism-based	Antagonistic, competitive, mutualistic	Model coefficient	Synthetic	Under certain conditions, a balance of different interaction types increases persistence of plant species interacting with mycorrhizal fungi and predators
Kéfi et al. 2016	Multilayer network analysed as an expanded food web model	Mechanism-based	Trophic and several non-trophic types	Frequency of interaction between species of the modelled guilds	Field surveys for species identification and expert knowledge for interaction assignment	Species are organized in clusters of interaction patterns, and this patterning enhances community persistence and robustness

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Fontaine et al. 2011	Multilayer network	N.A.	N.A.	N.A.	N.A.	Conceptual study on the consequences and challenges of merging two sub-networks
Pocock et al. 2012	Multilayer network	Mechanism-based	Trophic, mutualistic of several types and parasitic	Interaction frequency	Field surveys and published studies for assigning interactions	Different sub-networks varied in their robustness to random extinctions of plants
Evans et al. 2013	Multilayer network	Mechanism-based	Trophic, mutualistic of several types and parasitic	Interaction frequency	Field surveys and published studies for assigning interactions	Habitats of an agro-ecosystem contribute differentially to species and interaction diversity
Kéfi et al. 2015	Multilayer network	Mechanism-based	Trophic, positive non-trophic and negative non-trophic	Binary	Field surveys for species identification and expert knowledge for interaction assignment	Non-trophic interactions are more than twice as abundant than trophic ones, and show non-random structure

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Sander et al. 2015	Multilayer network	Effect-based (tatoosh island and doñana networks), Mechanism-based (norwood network, which differentiates herbivory and parasitism)	Three networks with different types	Binary	Different for each dataset	Accounting for different interaction types can improve groupings of species in interaction networks
Dáttilo et al. 2016	Multilayer network	Mechanism-based	Different types of mutualistic interactions	Binary	Field surveys for qualitative interactions	Multiple types of mutualism do not increase community robustness, but a few species contribute disproportionally to network structure.
Gracia-Lázaro et al. 2018	Multilayer network	Effect-based	Competition (intra-layer) and mutualism (inter-layer)	Model coefficients	Adjacency matrices from several plant-pollinator empirical networks	The intensity of mutualism and competition jointly influences species persistence
Pilosof et al. 2017	Multilayer network	N.A.	N.A.	N.A.	N.A.	Framework and examples for applying multilayer networks to ecological questions

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Bastolla et al. 2009	Equal footing network	Effect-based	Competition and mutualism	Model coefficient	Synthetic	Nested structure of mutualist networks increases community size
Melián et al. 2009	Multilayer network flattened to an equal footing model	Effect-based	Antagonistic and mutualistic sub-networks	Binary and relative interaction frequency (dependence)	Aggregated network from several studies	Empirical distributions of interaction type and strength generate more diversity than that of random networks
Almaraz and Oro 2011	Equal footing network	Effect-based	Negative interactions	Model coefficient	Abundance time-series	Body size effectively predicts the amount of population variance explained by interspecific interactions
Allesina and Tang 2012	Equal footing network	Effect-based	Single interaction networks and a mixture of competition and mutualism	Model coefficient	Synthetic	Predator-prey networks are the only ones that can be arbitrarily large and stable; other types increase their stability by decreasing average interaction strength
Mougi and Kondoh 2012	Equal footing network	Effect-based	Antagonistic and mutualistic	Model coefficient	Synthetic	Mixing antagonistic and mutualistic interactions and increasing complexity stabilizes model communities

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Mougi and Kondoh 2014	Equal footing network	Effect-based	Antagonistic, competitive and mutualistic	Model coefficient	Synthetic	Moderate mixing of the three interaction types, and food web structure in hybrid communities, promote stability
Sauve et al. 2014	Equal footing network	Effect-based	Antagonistic and mutualistic	Model coefficient	Synthetic	Connectance and diversity of mutualistic sub-network enhance overall stability; the reverse for antagonistic sub-network
Suweis et al. 2014	Equal footing network	Effect-based	Antagonistic and mutualistic	Model coefficient	Synthetic	Interaction mixing per se does not stabilize model communities; rather, the apparent stability comes from the 'constant interaction effort' hypothesis
Kondoh and Mougi 2015	Equal footing network	Effect-based	Antagonistic and mutualistic	Model coefficient	Synthetic	Stability is enhanced by mixing interaction types for communities with different proportions of constant and mixed interaction effort
Lurgi et al. 2016	Equal footing network	Effect-based	Antagonistic, mutualistic	Model coefficient	Synthetic	Increasing levels of plant-animal mutualistic interactions generally result in comparatively more stable communities

Study	Framework	Type of classification	Interaction types studied	Interaction strength	Type of data	Main findings
Mougi 2016a	Equal footing network	Effect-based	Antagonistic, mutualistic, competitive, amensalistic, commensalistic	Model coefficient	Synthetic	A mix of unilateral interactions (i.e. commensalistic and amensalistic) increases local stability
Mougi 2016b	Equal footing network	Effect-based	Antagonistic and mutualistic	Model coefficient	Synthetic	Adaptive shifting of interaction partners in hybrid antagonistic-mutualistic communities increases local stability
Sauve et al. 2016	Multilayer network flattened to an equal footing model	Effect-based	Pollination and herbivory	Binary and species' preference	Field surveys and published studies for assigning interactions	Empirical patterns of interactions promote local stability, but results differ when considering binary or quantitative networks
Sellman et al. 2016	Equal footing network	Effect-based	Antagonistic and mutualistic	Model coefficient	Synthetic	The frequency of functional extinctions is higher in mixed than single-type interaction networks

2.3 Expanded Food Webs

Food webs (networks of trophic interactions) represent the net flow of biomass or energy among individuals (Lindeman, 1942; Paine, 1966; Pimm, 1982; Moore and de Ruiter, 2012) and, more often than not, their constituent interactions are among the easiest to observe empirically. The study by Arditi et al. (2005) was probably the first in addressing the influence of other types of interactions in a large-scale food web framework. They assumed that non-trophic interactions affected the net interaction strength of consumer-resource relationships, modifying the net biomass flow from resources to consumers. The same idea was also addressed by Goudard and Loreau (2008) and, recently, Kéfi et al. (2012) expanded it to allow non-trophic interactions to influence any parameter of a food web dynamic model. These studies share the assumption that over the food web structure, there are other relationships that modify and constrain the resulting network by acting upon specific non-trophic ecological mechanisms.

As a minimal example, consider a general population dynamics model in which each species within a set S is parameterized only by an intrinsic growth rate term and a coefficient for its effect over each of the remaining species:

$$\frac{dN_x}{dt} = \left(r_x + \sum_{y \in S} a_{xy} N_y \right) N_x \tag{2.1}$$

where N_x is the abundance of species x, r_x its intrinsic growth rate, and a_{xy} the interaction coefficient of species y over x. With the framework proposed by Kéfi et al. (2012), each growth rate can be potentially influenced by a non-trophic interaction and, more generally, trait-mediated indirect interactions (Peacor and Werner, 1997) can be incorporated by modifying interaction strength parameters. Hence:

$$r_x \propto r_x^0 + \sum_{y \in S, y \neq x} q_{xy} N_y \tag{2.2}$$

$$a_{xy} \propto a_{xy}^0 + \sum_{z \in S, z \neq x, z \neq y} p_{xyz} N_z \tag{2.3}$$

where q_{xy} represents the per capita influence of species y on the growth rate of species x, independent of their trophic interaction coefficients, and p_{xyz} represents the per capita influence of species z on the interaction coefficient between species x and y.

Focusing on the biomass flow of the network, expanded food webs have the advantage that models complying with the principles of mass and energy conservation can be easily developed. As non-trophic interactions can influence any parameter of the dynamic model, the framework can accommodate detailed mechanisms of interactions taken from empirical observations or ecological hypotheses;

for example, the differential role of mutualistic interactions over different vital rates (Stachowicz, 2001). But not only vital rates can be modified: trait-mediated indirect interactions have been shown to have important effects on different ecological processes Golubski et al. (2016). As shown in Eq. 3, they can be seamlessly incorporated in this approach, since interaction strengths are usually constant parameters, just like demographic rates. The potential level of detail achievable with this framework, on the other hand, entails an unavoidable trade-off: for models involving just a few species, a vast number of parameters would have to be accounted for in order to have a complete model Golubski and Abrams (2011). For a food web of S species modelled after Eqs. 1-3, a full accounting of trophic interactions would yield S^2 interaction parameters plus S intrinsic growth parameters. Considering non-trophic influences over these basic parameters would add up to $S*(S-1)q_{xy}$ terms and either $S^2*(S-2)$ or $2\left(S^2*(S-2)\right)p_{xyz}$ terms depending on the symmetry of interactions, i.e. whether $x \to y = y \to x$ or not. In the simplest scenario of symmetric interactions, a total of S^3 parameters need to be accounted for. Further parameters would be needed if more sophisticated functional forms were to be considered (see, e.g., the Aire Island case study).

Note that similar approaches could be developed to take any other interaction type as the base of community structure. For example, for well-resolved mutualistic networks in which a certain plant species is consumed by another species, the effect of predation could be added to the mutualistic network by making the plant's mortality rate a function of the predator's abundance.
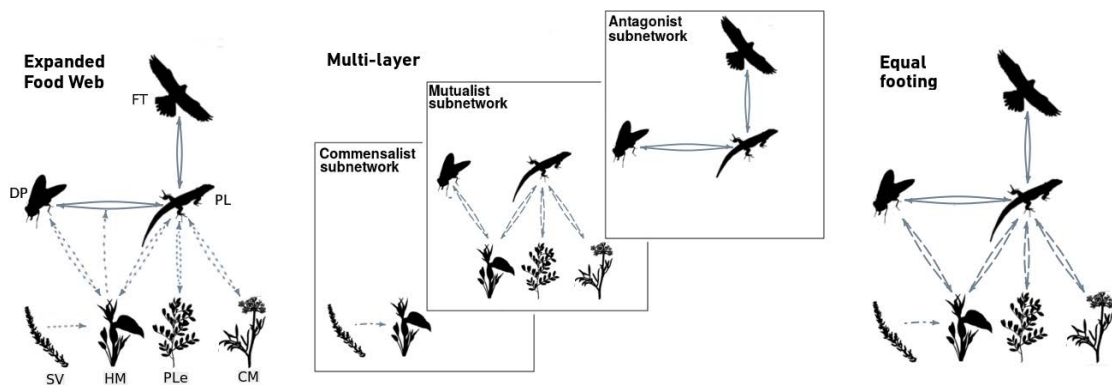
Figure 2.1: Three approaches for constructing and analyzing networks with multiple interaction types. In the first panel, solid lines represent trophic interactions, dotted lines non-trophic ones. Note that frugivory and pollination have both trophic and non-trophic components. In the second and third panels, solid lines represent antagonistic interactions, dashed lines mutualistic ones and dotted-dashed lines commensalistic ones. Data for building the network taken from the Aire Island community (see the Aire Island case study).

Multilayer Networks

The concept of networks formed by different types of interactions (edges, more generally, connecting two individual nodes of the network) was first developed in the first decades of the 20th century in the field of social sciences, for characterizing social interaction networks with different types of relationships between

individuals. Nevertheless, it is only in the last few years that the idea has been properly defined mathematically, given a consistent terminology, and applied to a wide variety of research objectives in, for example, engineering, economical or social networks (see the reviews by Boccaletti et al. 2014 and Kivelä et al. 2014 to learn more about the history, methodology and applications of the paradigm).

The basic principle is that nodes within a network can be linked in different ways or in different contexts, so that the overall network contains two or more layers that represent different link types or other aspects of variation. Nodes can be connected to nodes of the same layer (intra-layer links) or to nodes of different layers (inter-layer links). Such multidimensional object is called - in it most general definition - a multilayer network. An ecological community in which different species interact in a discrete number of ways is a very intuitive example of such a network Pilosof et al. (2017) each interaction type would constitute a different layer within the 'interaction type' aspect, and other potential layering aspects could be time (i.e. the realization of the network in different sampling campaigns) or site (different sampling plots).

Mathematically, a multilayer network consists on a quadruplet $M = (V_M, E_M, V, L)$. Its elements are, first, a sequence of sets of elementary layers $\{L_a\}_{a=1}^d$, where d is the number of layering aspects. The full set of nodes of the network, V , does not include the information about which node belongs to which layer, so a further set of node-layer tuples encodes this information: $V_m \subseteq V \times L_1 \times \cdots \times L_d$. These node-layer tuples, i.e. the instances of a node in a given layer, are called 'state nodes'. Lastly, $E_m \subseteq V_M \times V_M$ is the set of intra-layer and inter-layer links. This minimal definition is expanded in the reviews by Kivelä et al. (2014) and Pilosof et al. (2017). When designing multiple interactions networks, $d \geq 1$, as at least the layering relative to interaction type will be present; also, links may be constrained to 'diagonal coupling', i.e. the situation in which a node will only be connected to itself in different layers. Representations where layers are not interaction types but some other grouping of the community are also possible (Appendix 2.2). For modelling the dynamics of multilayer networks, any dynamical model representing species interactions may be used in which sub-networks are represented by sets of equations and, depending on the design, auxiliary equations may be used to connect the different state nodes of a given entity, or state nodes of different entities in different layers. The inter-layer links of a multilayer network make this framework particularly versatile, as these may represent any kind of relationship between layers (see Fig. A.2.2.3 for a definition of the different types of links in multilayer networks, and their matrix representation). For example, a link coupling the same plant species in pollination and herbivory sub-networks may represent the effect that consumption of reproductive organs by herbivores has in the interactions between the plant and its pollinators. Inter-layer links may also represent a coupling between layers with different temporal or spatial scales, thereby explicitly accounting for the temporal or spatial dimension of the networks. Note that this framework may accommodate networks with markedly different structures. For example, networks where virtually all links are intra-layer and the opposite, networks in which virtually all links are inter-layer, are both multilayer networks; also, networks whose nodes are present in every layer

or in just one of them can fall under this framework.

Multilayer networks have been explored in a few studies of multiple interactions networks (Table 2.1), but their applicability in ecology goes far beyond these studies. For example, they have been successfully applied to reconstruct super (phylogenetic) trees von Haeseler (2012), to study temporal and spatial variability in network structure, or to the analysis of ecological processes at different scales Pilosof et al. (2017) . Despite the potential of the multilayer framework for modelling ecological dynamics within and across layers, most studies listed in Table 2.1 have only analysed static structural patterns, with the only exceptions being the studies by Stella et al. (2016), who studied the dynamics of parasite spreading in multilayer ecological networks of varying structures, and by Gracia-Lázaro et al. (2018), on the influence of inter-layer mutualistic interactions over layers of competitive interactions. In general, ecological studies on multilayer networks are starting to show that interactions other than predator-prey ones are also highly structured (Melián et al., 2009; Kéfi et al., 2015) and this topological structure has important consequences for different community properties (Pocock et al., 2012; Evans et al., 2013; Kéfi et al., 2016).

As this approach has been developed mostly in theoretical physics and most reserachers in ecology may not be familiar with its terminology, a brief note is needed here. Following the definitions from Kivelä et al. (2014), a multilayer network is the most general object representing networks with multiple layering aspects and connections among layers. Although we focus on networks where the only layering aspect is interaction type and are diagonally-coupled, (termed 'multiplex' networks or 'edge-coloured multigraphs' in Kivelä et al. 2014), we acknowledge that multiple interactions networks can also include other layering aspects and more complex patterns of inter-layer links. Therefore we adopt the more general term of multilayer networks in our review (Box 2). We will also use indistinctly the 'layer' and 'sub-network' terms to refer to a layer of specific interaction types in this framework.

Equal Footing Networks

Regardless of the specific characteristics or vital rates of an organism potentially modified by a pairwise interaction, its effects can be summed up as influencing either (1) individual fitness, (2) population size, or (3) population growth rate (Abrams, 1987). This view of interactions as aggregating effects over general individual or population-level parameters is the conceptual basis behind 'equal footing networks', with the main consequence that pairwise interactions of any type can be measured and compared 'on equal footing'.

A minimal population dynamics model can be represented as in Eq. 1. The main difference with the expanded food webs is that here, trophic and non-trophic interactions influence the intrinsic growth rate through the interaction terms of the adjacency matrix $\left[a_{xy} \right]$, instead of being modelled through auxiliary equations 2-3. Therefore, the adjacency matrix may include all pairwise combinations {(0,0),(0,+),(0,-),(+,-),(+,+),(-,-)} (Fig. A.2.2.4).

Being a more general approach than expanded food webs, numerical models of equal footing networks are more scalable. Following Eq. 1, each species can be modelled by a single equation, and $S^2 + S$ parameters are required for a complete model of S species. This generality through the integration of fundamentally different interaction mechanisms in the adjacency matrix hinders the level of biological realism that can be achieved, in contrast with expanded food webs. By manipulating the signs of the adjacency matrix, different proportions of interaction types can be generated, but the effect of varying these proportions on community stability is an open question. Mougi and Kondoh (2012) showed that, under certain conditions, local stability is enhanced for theoretical communities mixing antagonism and mutualism, as opposed to communities with a single interaction type. Their a priori conditions were that 1) mutualisms and antagonisms have, in total, the same effect over population growth rates and 2) for any species, the net effect of a given interaction decreases with increasing numbers of links of the same type. Two subsequent studies debated their conclusions: (Suweis et al., 2014) stated that these conditions, and not the mixing of interaction types, were the factors that stabilized their models, whereas (Kondoh and Mougi, 2015) partially relaxed their initial assumptions and still found increasing stability with interaction mixing. Recently, the methodology developed in (Mougi and Kondoh, 2012) has been expanded to assess the role of commensalism and amensalism Mougi (2016a) and the potential switching of interactions Mougi (2016b), finding that separately accounting for these factors (unidirectional interactions and interaction switching) also increases local stability. The evaluation of equal footing networks through local stability analyses (for review see Table 2.1) is methodologically equivalent to the analysis of single-interaction networks. Hence, it is a natural approach for comparing networks of single and multiple interaction types without resorting to specific interaction mechanisms. In the studies already published (Table 2.1), different studies have considered different sets of interaction types and modelling assumptions, so that no integrative conclusions can be obtained at this point. Nevertheless, an emerging trend seems to be that networks with more than one interaction type and where different interactions are structured non-randomly are more locally stable than their single-interaction, non-structured counterparts.

The equal footing framework can be thought of as a particular type of multi-layer network, in which the interaction layers are 'flattened' in a single network, so that inter-layer links disappear, and each node is simultaneously affected by all interactions. This flattening is possible when three conditions are met: state nodes of the same node in the different layers of a multilayer network represent the same physical entity (as opposed to transportation networks, for example, where state nodes might represent bus or train stations of the same city), layers are diagonally-coupled, and all interactions in the different layers are expressed in the same units. This last condition is probably the most general, and in fact it represents our second criterion for distinguishing among frameworks. It allows the possibility of flattening multilayer networks in which there is link overlap among layers, as the overall effect will be a function of all layer-specific effects. We believe that these restrictive conditions, and the prevalence of equal footing networks in the theoretical studies listed in Table 2.1, merit the consideration

of this framework as separated from the more general multilayer networks. The study by Melián et al. (2009) provides an example of a multilayer dataset flattened to an equal footing dynamic model.

Box 1: Choosing a multiple interaction network methodology

What constitutes a 'realistic' representation of an ecological community? The answer is likely contingent on many factors, including the type of community being studied, the availability of empirical data and/or the ease to obtain it through observational or experimental studies. Although these factors, as well as research objectives and ecological assumptions, vary widely among studies, we propose a series of general guidelines for helping decide which multiple interactions framework is more appropriate for analyzing different types of data and questions (Fig. 2.1).

The first dichotomy is whether the study involves structural and/or dynamical analyses (in this context, dynamical analyses refer to model-based projections of, at least, species abundances or biomass). In the first case, countless studies have analysed network structure based on lists of species and presence/absence of interactions between them. An excellent example of a structural analysis of a multiple interaction network is the comprehensive study of the Chilean rocky shore intertidal community by Kéfi et al. (2015). We suggest, for such analyses, arranging data according to the multilayer framework, which provides a versatile representation of the network and for which there is a well established, wide set of diagnostic metrics (Pilosof et al., 2017).

When values of biomass/abundance and interaction strengths are sampled or estimated (for example, based on allometric relationships, as in e.g. Kéfi et al. (2016), community dynamics can be modelled. In these cases, the influence of the parameterization on the results obtained should be appropriately gauged against null models, but this topic is out of the scope of our study.

If interactions are classified in terms of their effect over a certain population parameter, either equal footing or multilayer networks are the appropriate modelling frameworks for analyzing dynamical systems. In this situation, choosing one approach over the other depends crucially on our second general criterion, i.e. the units in which interaction strengths are represented. Other factors may also play a role, for example the presence of multilink overlap (see case study), the complexity of inter-layer links, or whether the dynamics of single-interaction sub-networks may be of interest when considered as separate entities. Generalizing, if it is of any interest to consider interaction types separately (for example, if different interaction types are modelled through different functional forms and with different units) or there are complex inter-layer connections, multilayer networks should be used. If, on the other hand, the interest lies in the overall dynamics of the whole system, equal footing networks might be preferable.

The other branch of the flow chart in Fig. 2.2 represents the situation where estimates of interaction strength are classified according to the mechanism they act upon. In this case, if the community consists of relatively few species or functional groups, each interaction can be modelled in detail, and the number of parameters might still be manageable: expanded food webs provide the most appropriate framework for such situations. Modelling the dynamics of a higher number of species, on the other hand, usually implies less mechanistic knowledge of the interactions within the community, and therefore interactions can be grouped in layers of a multilayer network that represent specific families of mechanisms. Notwithstanding these guidelines, as before, other factors may play a role (e.g. the inclusion of interaction

modifiers, as in the case study). In all cases, selecting an appropriate framework will ultimately depend on the data at hand, the objectives of the study and the judgement and familiarity of the researchers with the different methodologies.
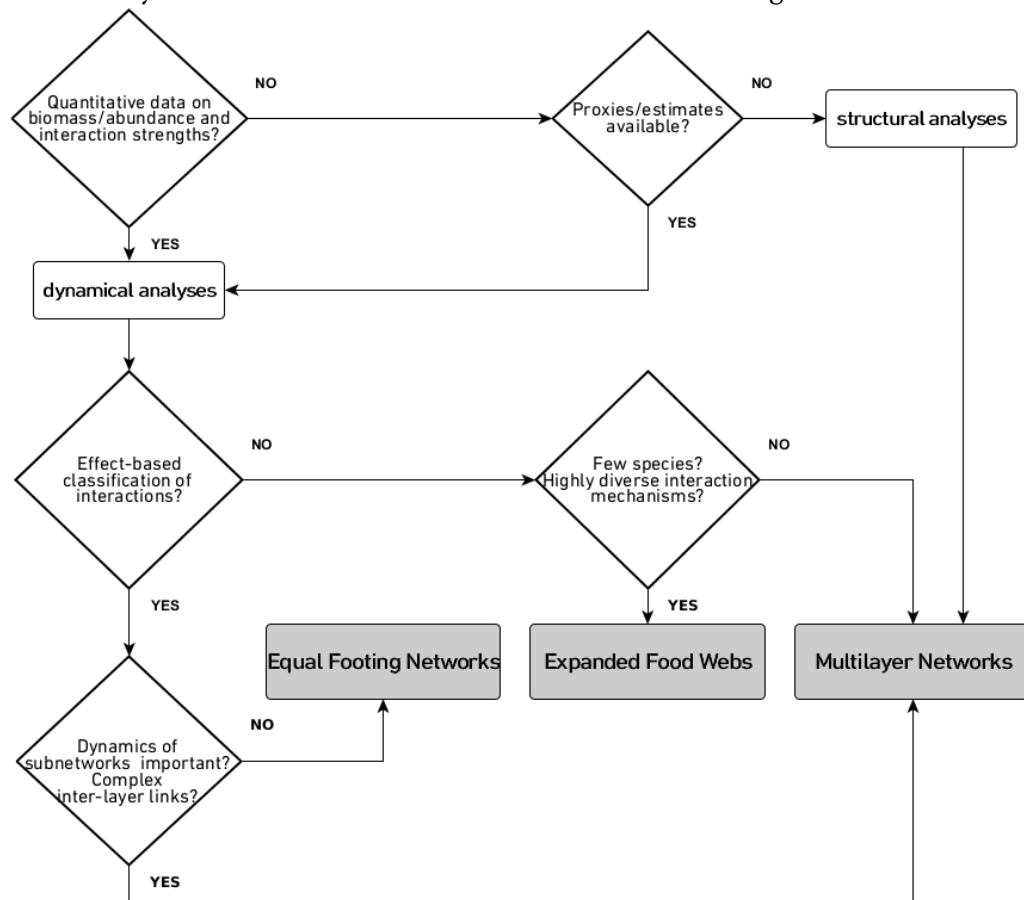
FIGURE 2.2: Diagram for choosing a multiple interaction network methodology, to be read starting from the upper left diamond box.

Acquisition and aggregation of empirical data

Collecting data on the presence and strength of pairwise interactions in nature is notoriously difficult, even for the most easily observed interactions (Jordano 2016). It follows that interaction networks tend to be markedly under-sampled (Chacoff et al., 2012), and the proportion of type II errors, i.e. existing interactions that are not observed, is rarely known (Olesen et al., 2011; Morales-Castilla et al., 2015; Gravel et al., 2016a). In turn, quantifying the strength of observed interactions is also a long-standing challenge even for single interaction networks (Berlow et al., 2004). Several interaction strength indices have been developed by theoretical ecologists, but these are usually disconnected from the set of metrics obtained in field or manipulative studies (Wootton and Emmerson, 2005). Furthermore, very few pairwise interaction types have been extensively studied and their functional forms analysed (e.g. Holland et al. 2002; Novak and Wootton 2008), while the existence and/or dynamics of the vast majority of interactions in nature remain unknown. Thus, designing and implementing programs for collecting reliable data

on multiple interaction types is presently one of the biggest challenges for community ecologists, up to the point that we are aware of just a handful of prominent examples in the literature. For example, Melián et al. (2009) aggregated data from several studies on pollination, seed dispersal and herbivory carried out between 1981-1984 in the Doñana Biological Reserve, in southern Spain. With that data, they constructed a network of 390 species and 798 interactions. Parasitic species and links, in addition to predator-prey interactions, were sampled by Hechinger et al. (2011) in food webs of three estuaries in the North American Pacific coast, in a dataset that included 314 species and 11270 interactions. In the study by Pocock et al. (2012), several interaction types were concurrently sampled in different habitats of an agro-ecosystem in the UK, obtaining a network of 560 species and 1501 interactions. Finally, two networks of intertidal communities have been collected recently: Sander et al. (2015) obtained 1898 interactions between 110 taxa from the intertidal middle zone of Tatoosh Island based on observations and natural history of the species, and Kéfi et al. (2015) took advantage of decades of work conducted on the marine rocky intertidal communities of the central Chilean coast to reconstruct its qualitative community network based on field observations and expert knowledge. Their network includes 104 species and 4754 interactions.

From these examples, one can distinguish two main strategies for constructing empirical multiple interactions networks: aggregating data from different sources of a given community in order to reconstruct the community network a posteriori (as in Melián et al. 2009; Hechinger et al. 2011; Kéfi et al. 2015 and Sander et al. 2015), or designing an integrated sampling program for a given set of previously defined interaction types, thus obtaining a realization of the network where all interactions are mostly co-occurring in space and time (as in Pocock et al. 2012). In the first approach, one may assemble information from studies conducted with different objectives and sampling methodologies and over different time periods, so that the aggregated network can potentially include a large fraction of the realized interactions, but these may or may not co-occur in time and/or space. Differential sampling efforts across studies will be unavoidable, and a posteriori analyses should be considered to minimize over or under-representation of certain clades and interactions. In the second approach, as fieldwork is likely to be conducted in tight time periods and in parallel for the different interaction types, sampling will potentially be more limited. On the other hand, this concurrent sampling is a more realistic snapshot of the co-occurring interactions in the sampling period, and importantly, fieldwork can be designed a priori to assign a near-homogeneous effort to different interaction types (but a posteriori corrections such as sample-based rarefaction are also advised; see Pocock et al. 2012 and references therein). A non-exhaustive list of factors to account for the design of field campaigns is provided in Table 2.2, but a more comprehensive analysis of sampling strategies for multiple interactions networks is needed.

Regarding the key issue of estimating empirical interaction strengths, it is often necessary to conduct manipulative experiments for obtaining reliable functional forms and interaction strength coefficients. Such experiments, however, are very context and clade-specific, and usually pose increased costs and logistical difficulties over field observations. For these reasons, a growing line of research is

Table 2.2: List of factors to consider in the design of sampling campaigns for multiple interaction types. These factors are general and independent from the framework chosen to represent the obtained network.

Factor	Examples of relevant questions
Temporal scale	Single sampling campaign or periodic samples? What is the time scale of the interactions to be sampled? Are all/certain interaction types expected to vary along the sampling period?
Spatial scale	What is the spatial scale of the interactions to be sampled? Are all/certain interaction types expected to vary spatially?
Habitat type(s)	How many habitat types will be sampled? How does sampling effort vary across habitats? Which interaction types are expected to be prevalent in each habitat type?
Interaction types	Which interaction types are expected to be sampled? Which sampling methodologies are applied to capture them? How does the proportion of forbidden links vary among interaction types?
Field and experimental observations	Are experimental observations needed for observing specific interaction types (e.g. for estimating the prevalence of parasitism, or the number of flowers visited by a given pollinator)? How is effort distributed among field and experimental observations?
Natural history of species	Do species in the community have varying activity periods or phenologies? Are there significant differences in mobility, behaviour, and other traits relevant to the probability of observing an interaction?
Movement capacity	Will network include permanent species or also transient ones? How is a permanent species defined?

being developed for, given minimal information, inferring the presence (Morales-Castilla et al., 2015; Deyle et al., 2016) and strength (Novak and Wootton, 2008; Berlow et al., 2009; Vázquez et al., 2012) of biotic interactions. Specifically, an interaction strength proxy that may be applicable to different types of interactions is the frequency of occurrence of an interaction. Poisot et al. (2015) proposed a general framework for integrating dynamic interaction strengths in dynamical models, taking into account the long-held idea that the net impact of a species over another can be described as a function of two components: the frequency of interaction and the per interaction effect (Vázquez et al., 2005). Thereby, the relative role of density-mediated and trait-mediated effects on direct interactions can be explicitly analysed. So far, it has been hypothesized that the net impact of mutualistic plant-pollinator interactions can be approximated by their frequency for both sides of the interaction (Vázquez et al., 2005, 2012) and, in addition, that the asymmetry among interaction strengths is well explained in some cases solely by species' relative abundances (for quantitative bipartite networks, as in Vázquez et al. 2007). These ideas converge towards a unified neutral view of ecological interactions: interactions can be approximated as being the result of random encounters among individuals, whose probability is mediated by the relative abundances of the populations involved (Araújo and Rozenfeld, 2014; Canard et al., 2012, 2014; Cazelles et al., 2016). The frequency of interactions will naturally equal the net impact of a population over another, since per capita interaction strength will not vary with other factors (traits, environmental conditions). Further research is needed to test the robustness of (1) species abundance as a proxy for interaction frequency, and (2) interaction frequency as a proxy for interaction strength.

Box 2: Definitions of key terms

The approach used for classifying interactions does not only have methodological consequences: it is above all constrained by the very definition of interaction. Hence, it is important to be clear and explicit about the definitions used.

The ones we use in this study for direct and indirect interactions are taken directly from Abrams (1987). These definitions can be applied both to effect-based and mechanism-based classifications, and though we define indirect interactions for completeness, we mainly focus on direct interactions.

For effect-based classifications, existing definitions are complete, as they cover the full spectrum of possible combinations of interactions in what can be described as the biotic interaction space (Araújo and Rozenfeld, 2014). New terms have been introduced with time, e.g. expanding the definition of (+,-) interactions originally described as being mainly characterized by predation to, first, contramensalism (Arthur and Mitchell, 1989) and later, antagonism (Sousa, 1993).

Within mechanism-based classifications the situation is somewhat more convoluted. In such studies, it is commonplace to study trophic and non-trophic interactions separately. Although defining these terms is apparently trivial, we have encountered very different implicit meanings of what constitutes a non-trophic interaction in the literature. For example, in the studies by Arditi et al. (2005) and Goudard and Loreau (2008), non-trophic interactions are defined as modifiers of trophic interactions. Prasad and Snyder (2010) consider non-trophic interactions to be 'driven by one species changing the behaviour but not the density of another species'. Finally, Kéfi et al. (2012) interprets non-trophic interactions as being all other interactions than feeding ones, including the non-trophic components of pairwise interactions such as pollination or frugivory. We adopt the latter definition, as it more clearly fits within a simple generalizable framework, although it requires certain interactions to be split in their trophic and non-trophic components. Lastly, effect-based and mechanism-based classifications need not be mutually exclusive (Abrams, 1987): it is common for effect-based interaction classes to be divided according to specific ecological mechanisms, e.g. mutualisms can be divided by considering whether there is a trophic component in them or not, etc.

Interaction A change in some characteristic of a population mediated by properties or actions by individuals of other population.

Direct interaction Interaction in which the effect occurs either through direct physical contact or through a third set of entities produced by one of the two interactors.

Indirect interaction Interaction in which the effect occurs as a result of other effects produced by one interactor on some population property of a third set of entities; and the third set of entities is not produced by any of the interactors.

Trophic interaction In the context of mechanism-based classifications, an interaction (or component of one) that involves direct exchange of energy (biomass) between the two individuals.

Non-trophic interaction In the context of mechanism-based classifications, an interaction (or component of one) that does not involve exchange of energy (biomass) between the two interacting individuals.

Single-interaction network Ecological network in which one interaction type is considered. Classic examples are food webs or plant-pollinator networks.

Multiple interaction network Ecological network with more than one interaction type. This umbrella term includes any topology and/or classification of interactions.

Expanded food web Multiple interaction network in which consumer-resource interactions form the basic structure of the network. Other interactions are termed "non-trophic" interactions and may affect any parameter of the dynamic model.

Multilayer network Network with different types of connections between nodes. In an ecological context, different network layers commonly represent different interaction types. If there is only one layering aspect and nodes are diagonally-coupled, that type of multilayer network is termed multiplex.

Equal footing network Multiple interaction network in which all interaction types are expressed in the same units, i.e. influence the same parameter of the dynamic model.

The Aire Island case study

The expanded food web, multilayer and equal footing frameworks for building multiple interactions networks offer complementary insights for the study of ecological communities, and each one is best suited to different types of studies and objectives (Box 1). Here, to demonstrate the diversity of ecological questions that can be addressed with multiple interactions networks, we analyse an empirical community under the lenses of each one of the approaches described. Specifically, we ask:

1. what is the influence of non-trophic interactions on the local abundances of all species? (expanded food web approach);

2. which species serve as "hubs" for linking species through interaction sub-networks and in the overall network? (multilayer network approach);

3. does the strength of different interaction types influences local community stability?(equal footing approach).

The community examined is located on the Aire Island, a small islet located SE off the coast of Menorca (Balearic Islands, Spain) with an area of around 342500 m². Almost the entire surface of this relatively flat islet is exposed to the effect of the sea. Therefore, most vegetation is halophilous (i.e. thrives in saline environments) except in areas sheltered from wind and sea, where typical Mediterranean species appear, such as Pistacia lentiscus (Pérez-Mellado et al., 2006). Our examples are based on a subset of the ecological community of this islet.

A remarkable set of interactions has been unveiled in the Aire Island between the dead horse arum (*Helicodiceros muscivorus*), its associated insect pollinators (Diptera, genus *Calliphora* and *Lucilia*), and the Balearic lizard, *Podarcis lilfordi*. The Balearic lizard is an omnivorous lacertid of medium size, endemic to the Balearic Islands. It has been shown to bask on the spathe of *Helicodiceros muscivorus* ' flowers, and to feed on the pollinating flies attracted by the intense odour produced by the plant. In addition to this negative effect of *Podarcis lilfordi* on *Helicodiceros muscivorus* through consumption of potential pollinators, it is itself an effective seed disperser of the plant: *Podarcis lilfordi* consumes ripe fruits of *Helicodiceros muscivorus* routinely, and seeds dispersed by the lizard show a significantly higher probability of germination than non-consumed seeds (Pérez-Mellado et al., 2006). *Podarcis lilfordi* is also an effective pollinator of other species at Aire Island. Particularly, high loads of pollen from *Pistacia lentiscus* and *Crithmum maritimum* have been found in lizard's bodies in previous studies on the same community (Pérez-Mellado et al., 2000). Due to the scarcity of natural predators, *Podarcis lilfordi* reaches high densities in the islet (Pérez-Mellado et al., 2008). Its main predator is probably the Eurasian Kestrel (*Falco tinnunculus*), that does not nest on the islet but visits it frequently. Lastly, the appearance of *Helicodiceros muscivorus* is related to the percentage of soil covered by *Suaeda Vera*, an hallophylous shrub of the Chenopodiaceae family, suggesting facilitation by the shrub on the development of *Helicodiceros muscivorus* (Pérez-Mellado et al., 2006). The interaction network formed by these 7 species (or guild, in the case of the Diptera) spans 3 trophic levels, and includes antagonistic, mutualistic and commensalistic interactions. In the following equations and figures, *S* refers to the whole set of species, and species are denoted by their initials or silhouettes. When available, we use empirical data for parameter estimates. Whenever empirically derived estimates are unavailable, as these examples are only to illustrate the approaches, we assign values based on our judgements of plausibility.

Expanded food webs: Influence of non-trophic interactions in equilibrium abundances

The main strength of the expanded food webs is the inclusion of detailed, mechanistic, non-trophic interactions in the general food web structure. We investigated their influence in the resulting abundance patterns of the community, compared to a standard food web model.

The continuous-time model for the expanded food web considers only three ecological processes: growth, mortality, and pairwise interactions, which can be trophic or non-trophic. Trophic interactions can, themselves, be modified by the presence of a third species. The main equations are of the form:

$$\frac{dN_x}{dt} = r_x N_x - m_x N_x^2 + \sum_{y \in S, y \neq x} a_{xy} N_x N_y \tag{2.4}$$

where r_x is the short-term per capita growth rate, m_x is the per capita mortality rate (that, multiplied by N_x^2, acts as a self-limitation term) and a_{xy} are the pairwise

trophic interaction coefficients (the partial derivative of the per capita growth rate of species x with respect to the density of species y).

Several non-trophic interactions are included on top of this general structure, affecting either r_x , m_x or a_{xy} . As an example, the modification of the mortality rate is modelled with a saturating function (Kéfi et al., 2012)

$$ m_x\left(N_y\right) = \frac{m_x^{NTI}N_y + m_x^0 N_y^0}{N_y + N_y^0} \tag{2.5} $$

The function varies between a basal value m_x^0 when $N_y = 0$, i.e. in the absence of non-trophic interactions, and m_x^{NTI} when the non-trophic interaction is highest. The same equation was used to model non-trophic interactions influencing the other parameters of Eq. 6 (growth rates r_x and interaction coefficients a_{xy}). For modelling the Aire Island community, we assumed that (1) all mutualistic interactions positively affect short-term growth rates, i.e. $r_x^{NTI} > r_x^0$ for *Helicodiceros muscivorus*, *Podarcis lilfordi*, Diptera, *Pistacia lentiscus* and *Crithmum maritimum*; (2) the presence of *Suaeda vera* increases the survival probability of *Helicodiceros muscivorus* seedlings by providing a favorable microhabitat, thus decreasing the mortality rate of the facilitated plant, i.e. $m_{HM}^{NTI} < m_{HM}^0$; and (3) increases in abundance of *Helicodiceros muscivorus* increased the magnitude of the predator-prey interaction between *Podarcis lilfordi* and the Diptera species, i.e. $a_{PL,DP}^{NTI} > a_{PL,DP}^0$ and $a_{DP,PL}^{NTI} < a_{DP,PL}^0$.

The complete parameterizations of the expanded food web model and the equal footing model are included in Appendix 2.1. We found significant differences in abundances at equilibrium for all species except *Suaeda vera*, depending on the set of interactions considered (Fig. 2.3). We define equilibrium as the steady state reached after a sufficient number of time steps (2500 in our case). Non-trophic interactions in the Aire Island community are all positive, and accordingly, all populations increase in equilibrium abundance when engaging in non-trophic interactions. The only organism that conceivably could be negatively affected by the inclusion of non-trophic interactions are the Diptera, given that the magnitude of the *Podarcis lilfordi* - Diptera antagonism is enhanced by higher abundance of *Helicodiceros muscivorus*. With the parameterization chosen, however, the positive influence of the Diptera – *Helicodiceros muscivorus* mutualism outweighs this increase (Fig. 2.3, note the increase in Diptera abundance when non-trophic interactions are considered). Note that this is the only approach in which we explicitly model the influence of *Helicodiceros muscivorus* populations in the predator-prey interaction between the Diptera species and *Podarcis lilfordi*.

Multilayer networks: Importance of each species in structuring the network

The role of the different species in structuring a given community has been extensively assessed for single-interaction networks (Coux et al., 2016) and for multilayer networks in other fields (Solé-ribalta et al., 2014; De Domenico et al., 2015). For the multilayer framework, several metrics have been adapted directly
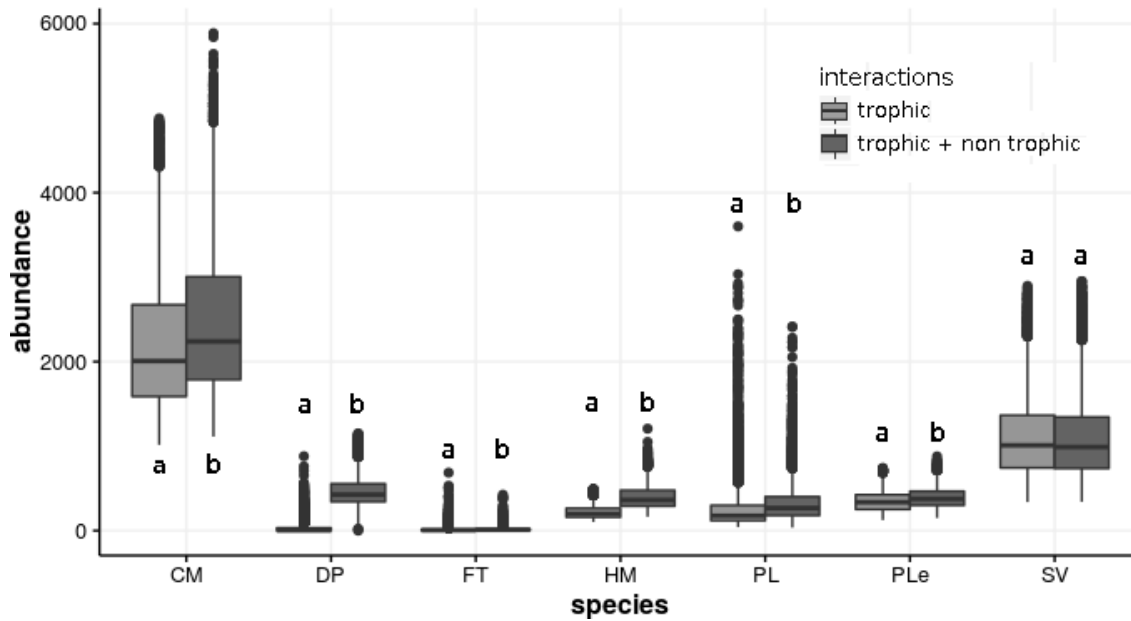
Figure 2.3: Equilibrium abundances of the Aire Island community when considering trophic interactions, or trophic and non-trophic ones. Boxplots with different letters are significantly different according to Wilcoxon rank-sum tests (CM: W = 38176000, p < 0.05; DP: W = 63730000, p < 0.05; FT: W = 38512000, p < 0.05; HM: W = 57170000, p < 0.05; PL: W = 42005000, p < 0.05; PLe: W = 38454000, p < 0.05; SV: W = 31595000, p = 0.059).

from single-interaction networks and others have been defined taking into account the multidimensional nature of the multilayer approach (De Domenico et al., 2015). Among these novel metrics, the concept of multidegree is a multidimensional extension of the degree of a single-interaction network, that may help uncover important, well-connected species in each sub-network and in the overall structure. Here we calculate multidegrees as defined in Boccaletti et al. (2014), where formal definitions are provided.

For understanding the concept of multidegrees, we first need to define the multilinks of the network. Multilinks (or multiedges) are links connecting two nodes in a combination of layers. For example, the Aire Island network has three interaction types. A multilink of the form (1,0,0) exists between two species if these species are connected in the first layer and not in the second or third one. One can see thus that the number of potential multilinks between any two species in a general network with M layers is 2^M. The multidegrees m_x^i of species i are its number of multilinks of type x, and its aggregation, m^i, is the overall multidegree as considered e.g. in Stella et al. (2016).

Given three layers representing interaction types {antagonism, commensalism, mutualism}, the multilinks for the Aire Island network are:

$$m_0 = \{0, 0, 0\}$$
$$m_1 = \{0, 0, 1\}$$
$$m_2 = \{0, 1, 0\}$$
$$m_3 = \{0, 1, 1\}$$
$$m_4 = \{1, 0, 0\}$$
$$m_5 = \{1, 0, 1\}$$
$$m_6 = \{1, 1, 0\}$$
$$m_7 = \{1, 1, 1\}$$

where m_0 is the null multilink, representing the situation in which two species are not connected in any layer, and subsequently, m_7 represents a multilink whereby two species are connected in the three layers. The number of shared multilinks between any two species can be represented by multi-adjacency matrices. The multi-adjacency matrices of the Aire Island community are:

$$A^{m_0} = \begin{pmatrix} & FT & PL & DP & HM & SV & PLe & CM & \\ 0 & 0 & 1 & 1 & 1 & 1 & 1 & FT \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & PL \\ 1 & 0 & 0 & 0 & 1 & 1 & 1 & DP \\ 1 & 0 & 0 & 0 & 0 & 1 & 1 & HM \\ 1 & 1 & 1 & 0 & 0 & 1 & 1 & SV \\ 1 & 0 & 1 & 1 & 1 & 0 & 1 & PLe \\ 1 & 0 & 1 & 1 & 1 & 1 & 0 & CM \end{pmatrix}$$

$$A^{m_1} = \begin{pmatrix} & FT & PL & DP & HM & SV & PLe & CM & \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & FT \\ 0 & 0 & 0 & 1 & 0 & 1 & 1 & PL \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & DP \\ 0 & 1 & 1 & 0 & 0 & 0 & 0 & HM \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & SV \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & PLe \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & CM \end{pmatrix}$$

$$A^{m_2} = \begin{pmatrix} & FT & PL & DP & HM & SV & PLe & CM & \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & FT \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & PL \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & DP \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & HM \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & SV \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & PLe \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & CM \end{pmatrix}$$

43

$$
A^{m_4} = \begin{array}{c} \\ \\ \end{array}
\begin{array}{ccccccc}
FT & PL & DP & HM & SV & PLe & CM \\
\end{array}
$$

$$
A^{m_4} = \left(\begin{array}{ccccccc}
0 & 1 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0
\end{array}\right)
\begin{array}{l}
FT \\
PL \\
DP \\
HM \\
SV \\
PLe \\
CM
\end{array}
$$

$$
A^{m_3} = A^{m_5} = A^{m_6} = A^{m_7} = 0
$$

The multidegrees of the seven species of the community are the number of multilinks incident to them (Table 2.3). These metrics show that *Podarcis lilfordi* is the most connected species, overall and both in the mutualist and antagonist sub-networks. *Helicodiceros muscivorus* and Diptera are the following species in multidegree, and their links also span two layers. All other species are represented only in one layer, and are only connected to *Podarcis lilfordi*, inviting the interpretation that the Balearic lizard has a disproportionate importance in structuring the community. In our small community, these results are visually evident, but the multidegree concept can be very useful in highly populated networks, where the importance of different species across layers is not obvious from visual inspection of the data. Note that by decomposing the overall multidegree into the contributions of each multilink we are able to evaluate the potential link overlap of any pair of species in any combination of layers. In our simple example, however, there is no overlap, a reasonable assumption when considering an effect-based classification of interactions over a single population parameter, since the potential partial positive and negative effects of a species over another are aggregated in order to calculate the net effect and the associated interaction type. For example, looking again at the *Podarcis – Helicodiceros* interaction, the net direct effect of the lizard over the plant could be decomposed in, at least, 1) a negative effect due to the consumption of fruits (i.e. the trophic part of the pairwise interaction), 2) another negative effect due to the predation of potential Diptera pollinators, 3) the positive effect on seed dispersal, and 4) a further positive effect on survival of seeds that have been dispersed by *Podarcis lilfordi* as opposed to seeds that germinate naturally. In the absence of more detailed experiments, and as suggested by Pérez-Mellado et al. (2006), we considered the overall effect of *Podarcis lilfordi* over *Helicodiceros muscivorus* to be positive. Link overlap in interactions can be expected when two species interact in different ways, for example due to varying ecologies of life stages, and more generally when the temporal dimension is included in the analyses.

Table 2.3: Multidegrees of the seven species of the Aire Island multilayer network. Note that the trivial m_0 multilink represents no connections, so it is not considered for calculating the overall multidegree m.

	m_0	m_1	m_2	m_3	m_4	m_5	m_6	m_7	m
Falco tinnunculus	5	0	0	0	1	0	0	0	1
Podarcis lilfordi	1	3	0	0	2	0	0	0	5
Diptera	4	1	0	0	1	0	0	0	2
Helicodiceros mus-civorus	3	2	1	0	0	0	0	0	3
Suaeda vera	5	0	1	0	0	0	0	0	1
Pistacia lentiscus	5	1	0	0	0	0	0	0	1
Crithmum maritimum	5	1	0	0	0	0	0	0	1

Equal footing networks: Influence of the magnitude of mutualistic and antagonistic interactions on community stability

For assessing the effect of the strength of different interaction types on the overall stability of the network, we modelled the community using the equal footing framework. We used the continuous-time logistic equations proposed by García-Algarra et al. (2014), in which all extrinsic effects – environmental, biotic interactions – fall on the intrinsic growth rate r_x :

$$\frac{dN_x}{dt} = r_x N_x \tag{2.6}$$

where

$$r_x = r_x^0 + \sum_{y \in S, y \neq x} a_{xy} N_y - \left(\beta_x + c_x \sum_{y \in S, y \neq x} a_{xy} N_y \right) N_x \tag{2.7}$$

The rightmost term of Eq.9 represents the self-limitation term. In the absence of pairwise interactions, the parameter β_x controls self-limitation, and c_x is a proportionality constant. Pairwise interaction coefficients a_{xy} were assumed constant. For assessing the relative influence of different interaction types on community stability, we varied the relative magnitude of facilitative (commensalistic and mutualistic interactions) and antagonistic coefficients and analysed the resulting local stability patterns of the system by examining the sign of the leading eigenvalue of the associated Jacobian matrix (Fig. 2.4 and Fig. A.2.3.2).

Parameterizations with weak antagonistic interactions were virtually all stable (19991 out of 20000 replicates), regardless of the magnitude of facilitative interaction strength (Fig. 2.4, groups a and b). Communities parameterized with strong antagonistic interactions (group c in Fig. 2.4), on the other hand, were mostly unstable, with only 20 out of 10000 replicates having a leading eigenvalue < 0. All unstable communities were also unfeasible in that either key species went extinct or some species grew unbounded despite the self-limitation term of

Eq. 9. Interaction strength magnitudes were chosen arbitrarily, in the absence of empirical data, but patterns were robust to variations of +- 2 orders of magnitude. Our results therefore suggest that increasing antagonist interaction strengths for this particular community would lead to instability. Bear in mind, though, that local stability analyses are only an approximation of ecological stability, as they only apply to closed systems in equilibrium. If accepting this assumption, local instability in the Aire Island community could be interpreted as being triggered by increased per capita antagonistic interaction strengths. These could appear, for example, if sexual dimorphism in *Podarcis lilfordi* led to higher predation of females by birds, thus exerting a higher influence on population growth rate. This, however, does not seem to be case, since the only dimorphism reported in Aire Island is the slightly larger body size of males (Pérez-Mellado et al., 2000); hence, no differential predation is expected.
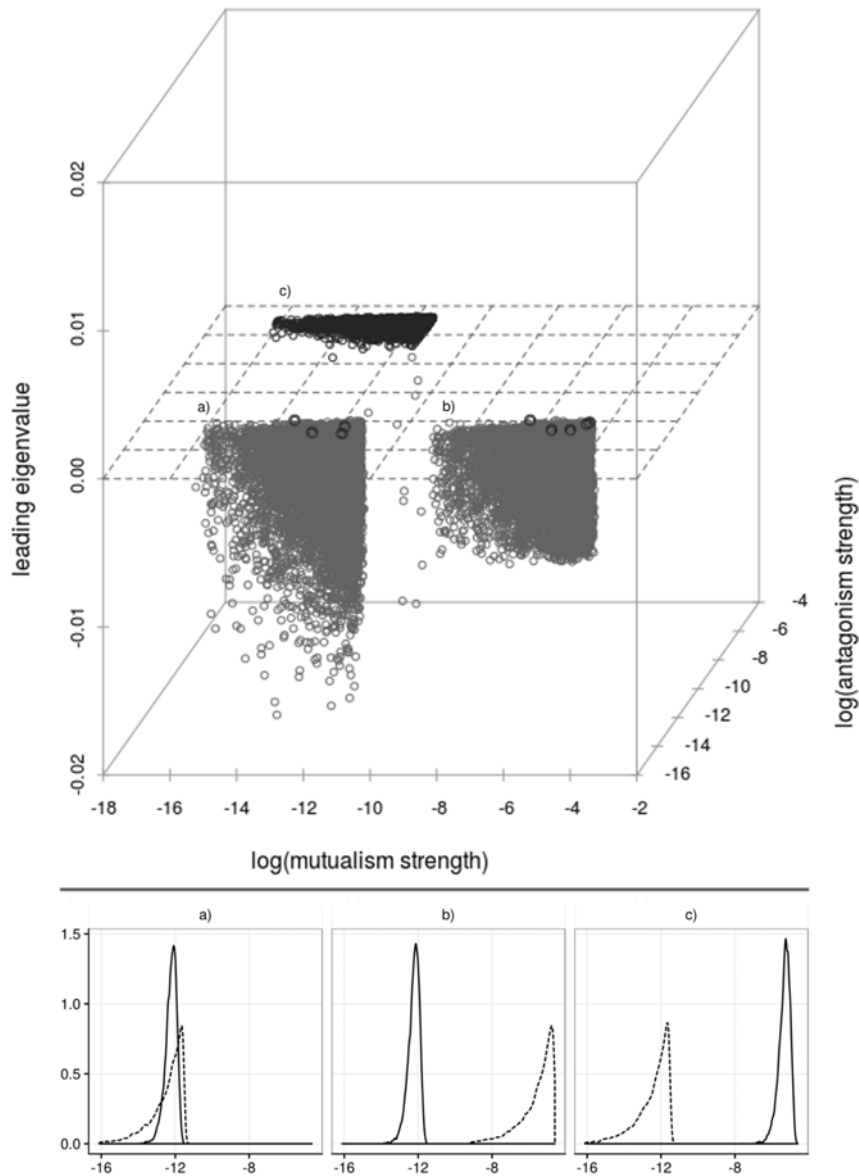
FIGURE 2.4: Distribution of antagonistic and mutualistic interaction strengths and the leading eigenvalue of the resulting system. In the scatterplot, grey circles are systems with leading eigenvalue ¡ 0, and black circles are systems with leading eigenvalue ¿ 0. Group a) is the group of simulations with weak antagonistic and facilitative interactions; group b) are simulations with weak antagonistic and strong facilitative interactions; group c) are simulations with strong antagonistic and weak facilitative interactions. Within group c) only eigenvalue magnitudes close to 0 are shown, due to the extreme variability of the raw data (with values up to $10^9 9$). The rest of the data is shown in Fig. A.2.3.2 . For reference, a grid is drawn representing the z = 0 plane. Lower panels show the density distribution, for each group, of the logarithm of antagonist interaction strengths (solid lines) and the logarithm of facilitative interaction strengths (dashed lines).

2.4 Lessons from the case study

In the Aire Island, the ecological community studied is structured around *Podarcis lilfordi*, due to its high density and its key role as omnivorous feeder as well as seed disperser and pollinator of several plant species. This species and

Helicodiceros muscivorus are the ones most connected in the network, as shown by the multidegree analysis. Non-trophic interactions are key for correctly projecting population abundances, supporting empirical observations of the importance of facilitation between plant species (Pérez-Mellado et al., 2006) and effective seed dispersal by *Podarcis lilfordi* (Pérez-Mellado et al., 2000). We posit that the role of non-trophic interactions, as modelled in the expanded food web approach, will vary among communities and studies, but it is essential to integrate them in food web analyses, particularly for fine-scale and well-studied systems. Lastly, with the equal footing approach, we have shown that if we assume all interactions to influence intrinsic growth rates, the strength of antagonistic interactions controls the local stability of the network by potentially driving *Podarcis lilfordi* or the Diptera pollinators to extinction. Specifically, even if no local extinctions occur, the variability on the *Podarcis* abundances driven by an increase in antagonistic interaction strengths can destabilize the community, due to its central position on the network (as shown by the multidegree analysis). Positive interactions, in turn, can vary in magnitude without significant effects on local stability.

The results shown here, however, are merely to exemplify the application of the three methodologies on different ecological questions. Different methodologies evaluating the same problem may yield varying results; for example, equilibrium abundances of stable simulations obtained with the equal footing approach (Fig. A.2.3.1) vary significantly from those obtained with the expanded food webs (Fig. 2.3). Choosing an appropriate formulation is not an exact science, as it involves a balance between available spatiotemporal data on species and interactions, natural history knowledge of the system, parsimony of the mathematical model, and objectives of the study (Box 1). In this particular community, in which the number of species is limited and the main interactions and mechanisms are relatively well-known, we advocate for more in-depth analyses based on expanded food webs, that may be parameterized with the results of manipulative studies of, e.g. localised removal of certain species or seed dispersal experiments for obtaining estimates of interaction strength.

2.5   Network ecology moving forward

Communities are comprised of individuals of different species interacting dynamically, and the wide variety of interactions any species engages in is key to its survival and thriving. Incorporating the effects of multiple interaction types in network analyses provides a more complete picture of community dynamics than relying on networks of a single interaction type. We have shown that frameworks for the study of multiple interactions networks are sufficiently mature and can accommodate a wide variety of research objectives and types of empirical data. We hope that the improved understanding of these frameworks, and the explicit recognition of their relative limitations and advantages, will lead to designing field studies that adequately capture the variety of interactions in communities, thus going beyond traditional approaches focusing on single interactions and often single clades. Questions in community ecology that remain unanswered can be addressed with a multiple interactions networks approach to the analysis

of ecological communities. For example, we have little knowledge regarding the proportion among different types of interactions in real communities, whether this proportion is constant, whether it varies with any intrinsic or extrinsic factor, or whether it is related to community stability. Furthermore, it is unclear whether the trophic position of a species is related to the type of interactions it is more likely to be engaged in. Likewise, we have little knowledge of whether a species deemed important in a given sub-network will generally have such a role in sub-networks of other interaction types. Because observation of interaction strength in natural systems is extremely difficult to document, integration of empirical data and modelling frameworks requires that consistent interaction strength proxies be designed and tested. The neutral interactions hypothesis is a promising starting point for providing a metric applicable to all interaction types, but it needs to be tested for different communities and interaction types. On the other hand, the application of expanded food webs models to specific communities can trigger the design of manipulative studies to assess the functional forms and dynamics of non-trophic interactions, most of which remain unknown despite their importance.

These and other related questions are fundamental in order to understand the response of ecological communities to perturbations such as climate change or habitat loss. In summary, the development of theoretical models, such as the ones presented here, needs to be contrasted with multipe field or experimental studies for different community types.

The effect of multiple biotic interaction types on species persistence

Abstract

No species can persist in isolation from other species, but how biotic interactions affect species persistence is still a matter of inquiry. Is persistence more likely in communities with higher proportion of competing species, or in communities with more positive interactions? How do different components of community structure mediate this relationship? We address these questions using a novel simulation framework that generates realistic communities with varying numbers of species and different proportions of biotic interaction types within and across trophic levels. We show that when communities have fewer species, persistence is more likely if positive interactions—such as mutualism and commensalism—are prevalent. In species-rich communities, the disproportionate effect of positive interactions on persistence is diluted and different combinations of biotic interaction types can coexist without affecting persistence significantly. We present the first theoretical examination of how multiple-interaction networks with varying architectures relate to local species persistence, and provide insight about the underlying causes of stability in communities.

3.1 Introduction

Persistence of multicellular organisms depends on interactions with other organisms, whether they be in the form of energy intake, use of habitats created by other species, assistance in reproduction by directed dispersal of genetic material, or countless other examples (Bascompte and Jordano, 2007). Ecological communities can be represented as networks, whereby species or guilds are nodes connected by links representing interactions (Proulx et al., 2005). Pairwise direct interactions can have positive, negative or neutral effects on the species involved, and this classification gives rise to five general types of interactions: amensalism (-,0), antagonism (+,-), commensalism (+,0), competition (-,-) and mutualism (+,+). Despite the wealth of empirical observations of biological interactions in nature, there still exists limited understanding of the frequency with which different types of biotic interactions occur in communities, and the consequences for community structure and functioning. For example, is the frequency of interaction types in communities related to overall persistence of species locally? Does the structure of the different interaction types play a role in increasing the odds of species persistence? Answering these and other questions has been hampered by difficulties in simultaneously sampling different interaction types in natural systems. Consequently, most studies have been based on observations of single interaction types within networks, which obviously has limited the ability to generalize beyond particular cases.

This fundamental gap in the understanding of ecological networks has been largely acknowledged (Strauss and Irwin, 2004; Agrawal et al., 2007; Ings et al., 2009; Fontaine et al., 2011), and there is increasing evidence that accounting for different interaction types generates novel insights on the structure and dynamics of ecological communities (Pilosof et al., 2017; García-Callejas et al., 2018b). Analyses of networks with multiple interaction types have already been applied,

for example, to investigate the distribution of the different interaction types and its relationship with species traits (Kéfi et al., 2015, 2016) or the robustness of communities to local extinctions and habitat loss (Pocock et al., 2012; Evans et al., 2013). Recent studies have also focused on investigating the relationship between the diversity of interaction types and several facets of community stability, often reaching different conclusions over this relationship. For example, it has been proposed that 1) mixing of interaction types generally increases local stability of model communities (Mougi and Kondoh, 2012, 2014; Kondoh and Mougi, 2015), 2) mixing of interaction types generally decreases local stability of model communities or increases the number of functional extinctions (Suweis et al., 2014; Sellman et al., 2016), or 3) structural factors of the different sub-networks enhance or decrease their stability (Melián et al., 2009; Sauve et al., 2014, 2016). The conflicting results over this fundamental question can be explained by the sheer diversity of modeling assumptions, structural constraints, and varying sets of interaction types included in the studies. For example, several studies (Melián et al., 2009; Sauve et al., 2014, 2016) analyzed communities consisting of only antagonistic and mutualistic interactions in which a central group of species (usually plants) is the guild connecting the mutualistic (e.g. plant-pollinator) and antagonistic (e.g. plant-herbivore) networks. Other studies considered model communities with only basic rules about food web structure (Mougi and Kondoh, 2012; Suweis et al., 2014). A common feature of most studies is that, with the exception of Mougi (2016*a*), their models did not consider the five general interaction types concurrently. However, Mougi (2016*a*) only analyzed random interaction matrices in his model, making his conclusions difficult to contrast with those of other studies that assumed stronger structural constraints. The role of species richness in mediating community stability also has been extensively studied in single-interaction networks, and analytical derivations have been produced for idealized conditions in mutualism-competitition networks (Allesina and Tang, 2012). In most cases, theory shows that increasing richness decreases local stability of random networks, but it is unclear how species richness mediates different facets of stability in networks with more complex structures and varying proportions of interaction types.

All in all, while approaches assessing the local stability of random interaction networks have important heuristic value (Allesina and Tang, 2012; Allesina et al., 2015), such randomly assembled networks lack key structural patterns found in real communities (Jacquet et al., 2016). Furthermore, local stability analyses have little concordance with non-equilibrium dynamics of real systems (Pimm, 1982; Chen and Cohen, 2001), which limits their predictive ability. The equilibrium assumption is further ingrained in most interaction models by assuming that interactions occur with a constant strength coefficient. This assumption is widely used for convenience despite repeated claims against its realism (Abrams, 1980, 2001; Hernández, 1998; Holland and Deangelis, 2009). Here we address all the above-mentioned shortcomings and investigate whether the frequencies of the five biotic interaction types affect persistence of species in communities with varying species richness. We generate model networks informed by empirical observations on distributions of species abundances across trophic levels, link topology, and develop a measure of the impact that a species has over another

based not on static interaction coefficients, but on species abundances and their associated frequency of interaction. With this model design, and by performing a comprehensive set of simulations, we ask the following questions: 1) Is species persistence affected by the frequency of the different interaction types in model communities? If so, does community richness mediate this relationship? 2) Which types of biotic interactions are more likely to be lost, as species go locally extinct? Lastly, given the unfeasibility of validating our predictions with empirical data, we indirectly test the validity of our model by asking: 3) does our model generates community-level patterns consistent with those of empirical networks?

3.2   Methods

We designed a dynamic network model accounting for the five possible types of pairwise interactions (antagonism, amensalism, commensalism, competition, and mutualism), whereby the impact of a species over another is characterized by the abundances of the species involved. Accounting for different interaction types meant that a trophic level distribution of species had to be specified a priori, as we expected different interaction types to be distributed unevenly across trophic levels. Furthermore, the modeling of pairwise interactions in our model is closely linked to the abundances of the interacting species, so we imposed non-random initial abundance values. In particular, we assembled our model communities with three assumptions:

1) The initial Species Abundance Distribution of the overall community follows a hollow curve.

2) The initial abundances of the different trophic levels vary with a power-law scaling.

3) The distribution of interaction types within and across trophic levels is non-random.

In the following sections, we describe these assumptions and the methodology for incorporating them in the community assembly process. Then, we specify the implementation of the dynamic interactions model and the simulations performed. The main response variable obtained from our simulations is the ratio of persistent species in our model networks. Thus, in the context of the present study, we define community persistence as the ratio between initial (denominator) and final (numerator) number of species in a simulated community. Persistence values can therefore range from 0 (all initial species have died out by the end of the simulation) to 1 (all species show positive abundances at the end of the simulation).

1) Abundance distribution of the overall community

Each species within a model community was assigned an initial abundance by drawing random samples from a gambin distribution. The gambin is a distribution with a single free parameter that provides a similar or better fit to empirical SADs than classic choices such as the lognormal or the logseries (Matthews et al., 2014). A value of $\alpha = 2$ was given to generate the initial SADs.

2) Abundance scaling across trophic levels

Species were distributed among four trophic levels (a basal one consisting on primary producers and three consumer levels), which is a number commonly found in empirical communities (Ulanowicz et al., 2014). Assignment of species into each trophic level was made following the findings of Hatton et al. (2015), who showed that for herbivore-predator trophic guilds, biomass distribution follows a power law with exponent 0.75. These authors generalized the scaling rule to the abundance of species at each trophic level since, for most predator-prey couplings, weak relationships between body mass and community biomass were found. As a starting working hypothesis for the simulations, we extended Hatton's et al (2015) scaling rule to the four trophic levels considered.

3) Distribution of interaction types within communities

The different types of biotic interactions are unlikely to be uniformly distributed in nature. Yet little is known regarding the varying proportion of interaction types within communities or trophic levels (Dodds, 1997), let alone about changes in such proportions across communities, or the effects of varying proportions of interaction types on mechanisms of community assembly.

A first step towards examining the frequency distribution of the different interaction types in a community with several discrete trophic levels is to consider the sign matrix of the community, S, assuming that interaction signs are kept constant within the spatial and temporal limits of the study, and with varying abundances. We hypothesize that the relative frequency of each interaction type in S will be influenced by the number of species in the different trophic levels, as different interaction types will have different probabilities of occurring among species belonging to the same or different trophic levels. In order to check this working hypothesis, we undertook an extensive survey of literature on biotic interactions and compiled the extent to which the five general interaction types (amensalism, antagonism, commensalism, competition, mutualism) are documented to occur between species of the same, adjacent, or non-adjacent trophic levels. Specifically, we performed a search in the Web of Science for studies published from 1991 to 2015, including the terms "ecology" AND "interaction" AND "interaction type" (see also Morales-Castilla et al. 2015). We reviewed studies documenting direct pairwise interactions and annotated the trophic level of the species involved. For competition, antagonism (predation OR herbivory), and mutualism, we included *ca*. 100 papers. For commensalism and amensalism the list of suitable studies was more reduced (67 studies on commensalism and only 12 on amensalism). We constrained the results by discarding interactions involving microorganisms, fungi, parasites or parasitoids, owing to the overall difficulty of classifying these groups into clear cut trophic levels. The list of selected studies is available as online supplementary material in the published article, see section *Chapter references* for the full reference. The resulting relative frequencies (Fig. 3.1) were incorporated as a last constraint in the model in the form of probabilities of pairwise interactions taking place within a single trophic level, adjacent, or other trophic levels.

For estimating the number of links of each species, we followed the constant connectance hypothesis (Martinez, 1992). Thus, we assumed no variation in connectance levels with initial community size, imposing C = 0.5 for every simulation, where connectance is defined as the ratio between realized and potential interactions in the network. This value was chosen so that specific connectances of the different interaction types (see Appendix 3.4) ranged between 0.07 and 0.2, values consistent with empirical estimates of mutualistic and antagonistic connectance (Thébault and Fontaine, 2010).

With the probabilities of interaction occurrence across trophic levels (Fig. 3.1) and connectance values of the network, we constructed the sign matrices of our model communities stochastically: for each link, first its interaction type is selected; second, the trophic levels affected by that interaction are chosen according to the probabilities of interaction occurrence; and third, the specific species are randomly chosen. This process ensures that, on average, sign matrices will reflect the probabilities of Fig. 3.1, while allowing for an intrinsic component of variability in each particular matrix. The full community assembly process is explained in detail in Appendix 3.1.
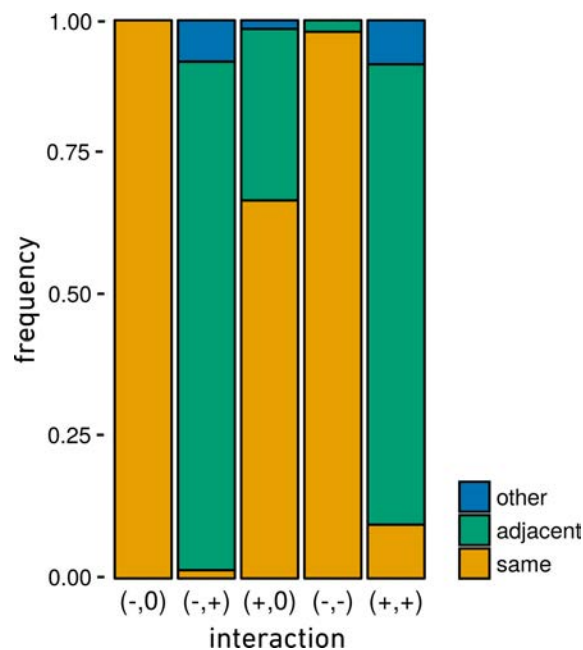
FIGURE 3.1: relative frequency of trophic levels involved in pairwise interactions for each interaction type. When the trophic level of the interacting species was not explicitly alluded to, we assumed that 1) species of the same taxonomic group belong to the same trophic level (e.g. isopods), 2) omnivory represents feeding on both "adjacent" and "other" trophic levels, 3) pollinators and seed dispersers are "adjacent" to plants. $N_{amensalism} = 12$, $N_{antagonism} = 135$ (123 of adjacent trophic levels, 10 of other, 2 of same), $N_{commensalism} = 65$ (44 of same trophic level, 20 of adjacent, 1 of other), $N_{competition} = 97$ (95 of same trophic level, 2 of adjacent), $N_{mutualism} = 113$ (94 of adjacent trophic levels, 11 of same, 9 of other).

A framework for modeling dynamic interactions

The realization and outcome of direct pairwise interactions is dependent on three classes of mechanisms (Poisot et al., 2015): First, the frequency of stochastic encounters of individuals mediated by their relative abundances. Second, the matching of traits between individuals that establish contact. Third, other factors such as environmental constraints or the influence of higher order interactions with other species. Hence, empirical measurements of interactions show a high degree of variability explained, partly, by density-dependent mechanisms (Aizen et al., 2014), by trait matching (Santamaría and Rodríguez-Gironés, 2007) or by environmental factors (Mazía et al., 2016; Poisot et al., 2017). This inherent variability on both the sign and the strength of interactions has hardly been explored in community dynamic models, even if the assumption of static interaction sign and strength is known to be unrealistic (Abrams, 1980, 2001; Hernández, 1998; Holland and Deangelis, 2009). The importance of each mechanism in explaining observed patterns of interaction strengths is currently under debate. In plant-pollinator networks, for example, the net impact of a species over another is significantly related to the frequency of interaction (Vázquez et al., 2005, 2012), and to the abundances of the interacting species (Vázquez et al., 2007), but not in all cases. A neutral model of interactions can also reproduce structural patterns observed in empirical food webs (Canard et al., 2012). On the other hand, trait-matching has been shown to accurately reproduce network structure in different types of networks (Eklöf et al., 2013), and also outperforms neutral interaction frequency for predicting network structure in some empirical networks (Vizentin-Bugoni et al., 2014; Sazatornil et al., 2016). However, another recent study showed that while abundances and traits can predict network structural patterns, they were not generally able to predict the realization of specific interactions in a plant-pollinator network (Olito and Fox, 2014). Finally, higher-order influences on interaction occurrence and strength, in particular environmental forcing, are a main focus of Stress Gradient Theory (Maestre et al., 2009) and Environmental Stress Models (Menge and Sutherland, 1987), but an integration of these frameworks with the recent advances on multi-trophic, multiple interactions networks is still lacking.

We modeled the impact of a species over another by considering the first of these three mechanisms, i.e. the stochastic encounters between individuals of two populations driven by their abundances. This process is the only one that can be generalized to any interaction and community type without considering further, specific assumptions about trait distributions or the role of environmental covariates. Thus, in our modeling framework, the impact of a species over another is only dependent on the frequency of interaction between the two species, which in turn depends on their net abundances. As our approach is fundamentally different to that of models with static interaction strength coefficients, we refer to the interaction strength in our model as species impact (a population-level effect, Vázquez et al. 2012).

In formulating species impact, we followed Poisot et al. (2015) and considered

it a product of interaction frequency by an interaction strength term:

$$I_{i,j} = IF_{i,j} * IS_{i,j} \tag{3.1}$$

The IF function derives the net frequency of interactions between two populations in a given time interval from their local abundances. We assume that (1) the maximum potential interaction frequency will equal the population density of the least abundant species, and (2) interaction frequency saturates asymptotically, as one or both abundances increase. It takes the form:

$$IF_{i,j} = min(N_i, N_j) \frac{1}{1 + e^{-a(max(N_i, N_j) - x_0)}} \tag{3.2}$$

The a parameter adjusts the saturating behavior of the function (i.e. its steepness), so that a higher value of a implies that the IF function saturates at lower abundances of both populations, i.e. interactions are comparatively more common. Parameter $x0$ indicates the abscissa of the midpoint for the logistic part of the function, and was kept for reference.

The IS function (for interaction strength) models the sign and strength of per capita interactions of species j over species i. This function was defined just as the sign of the pairwise interaction times a scaling factor for differentiating interaction types. For example, a scaling of 1 indicates that the maximum effect of species j over species i is of the same order of magnitude as the population growth rate. Therefore, we defined the IS function simply as:

$$IS_{i,j} = s_{i,j} * k_t \tag{3.3}$$

where $s_{i,j}$ is the sign of the effect of species j over species i, and k_t is the scaling factor for an interaction of type t.

We incorporated Eq. 3.1 to a population dynamics model based on the recent extensions to the logistic growth equation by García-Algarra et al. (2014). Their formulation averts a known divergent behavior of the r-k classic form of the logistic equation and is sufficiently simple while being able to reproduce the complexity of more elaborate models in terms of fixed points and stabillity of the dynamics. Consider a community of n species. The model has the form:

$$\frac{dN_i}{dt} = r_i N_i \tag{3.4}$$

whereby all extrinsic effects – environmental, biotic interactions – fall on the intrinsic growth rate r_i. This allows the comparison between the strength of different interactions, i.e. it is an example of an equal footing network (García-Callejas et al., 2018b). The effective growth rate is modeled as:

$$r_i = r_i^0 + \sum_{j=1, j \neq i}^{n} I_{i,j} - (\alpha_i + c_i \sum_{j=1, j \neq i}^{n} I_{i,j}) N_i \tag{3.5}$$

where r_i^0 is the intrinsic growth rate, α_i is the friction term that regulates the asymptotic behavior of the function, c_i is a proportionality constant, and $I_{i,j}$ is the impact function from Eq. 3.1.

Simulations

We generated theoretical communities with 20,40, and 60 initial numbers of species that corresponded to overall abundances of around 2395, 4640 and 6850 individuals, respectively. For each richness level, we defined six types of communities according to the frequency with which the different interaction types occurred: equal ratio type with relative frequency of 0.2 for every interaction type; and five types in which each of the interaction types was the most prevalent (with frequencies of 0.4 for the prevalent type and 0.15 for the others). We projected the dynamics of 1000 replicates for each of these combination of factors, ending up with $3 * 6 * 1000 = 18000$ simulated communities. For each replicate, aside from the inherent stochasticity of the assembly process, we drew the intrinsic growth rates and saturation terms of each species (r_i^0 and α_i from eq. 3.5) randomly from an interval of potential values (Table A.3.1.4), ensuring that primary producers have intrinsic growth rates $r_i^0 > 0$ and consumers $r_i^0 < 0$. Introducing these stochastic components on the assembly process and parameterization enabled us to test the robustness of the model to small variations in its initial conditions. The full parameterization of the model, alongside with further details about its implementation and numerical solving, is given in Appendix 3.1. Preliminary tests showed that most simulated communities reached a stable abundance distribution after 2500 or less time steps but, conservatively, we ran our dynamic model for 5000 time steps. In order to be more confident on the time steps chosen, we also tested whether there were significant differences between the resulting persistence patterns after 5000 and 10000 time steps. As no significant differences were found, we considered 5000 time steps to be an appropriate time frame for our simulations.

We also performed additional simulations in order to test the influence of the imposed structural constraints in our results. In these simulations we relaxed, one by one, the three constraints of the community assembly process (see Appendix 3.3 for more details).

3.3 Results

Is species persistence influenced by the frequency of the different interaction types? If so, does community richness mediate this relationship?

Model communities with a higher proportion of positive interactions (mutualism and, to a lesser extent, commensalism) tended to have higher species persistence than any other community type (Fig. 3.2, results of statistical tests in Table A.3.2.1 and Table A.3.2.2). The effect of positive interactions on persistence was strongest for species-poor communities, and decreased consistently as the

numbers of species in the communities increased. Although average species persistence converged to around 88% as richness increased, there was significant variation between the persistence of species belonging to the different trophic levels (Fig. A.3.2.1): in communities with low initial richness, the second and third trophic levels saw more extinctions than the first, while species on the fourth trophic level did not show a uniform behavior, and were more dependent on variations in the relative frequency of interaction types. This general pattern was reversed in more speciose communities, in which species of all higher trophic levels showed more persistence than the basal ones, for all community types.

Supplementary simulations (Appendix 3.3) showed that persistence values are further influenced by the community structural patterns imposed. The removal of both the abundance scaling across trophic levels and the distribution of interaction types across trophic levels had a significant negative effect on persistence. Sampling species abundances from a uniform SAD instead of a skewed one, on the other hand, increased overall persistence.
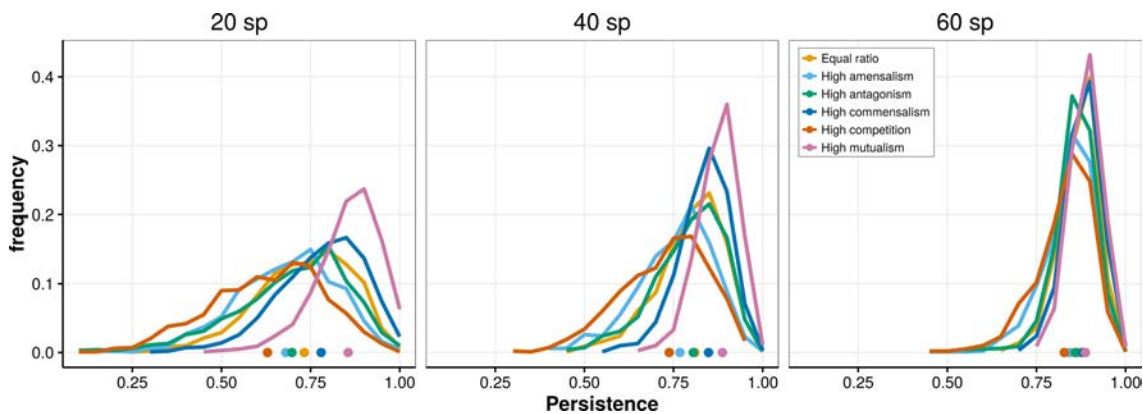
Figure 3.2: Persistence values of the simulated communities at the end of the simulations. Vertical axis represents the relative frequency of a given persistence value in the pool of replicates (1000 replicates for every combination of initial richness and initial frequency of interaction types). All resulting pairs of persistence distributions but one are significantly different according to Kruskal-Wallis rank tests (Table A.3.2.1) and post-hoc Dunn's tests (Table A.3.2.2).

Which types of biotic interactions are more likely to be lost, as species go extinct?

In our model, local extinctions have structural consequences for the remaining network: when a species goes extinct, its interactions disappear as well and are not replaced. The initial and final frequencies of the different interaction types were significantly different in most cases (Fig. 3.3, results of statistical tests in Table A.3.2.3). Amensalism and competition tended to decrease in relative frequency with respect to initial levels, while mutualism tended to increase. Antagonism and commensalism responded differently for varying levels of community richness. Antagonistic interactions decreased in frequency only in communities with 20 initial species, while in communities with 60 species, they increased; the opposite

was observed for commensalism, which increased in species-poor communities but decreased with high species richness.
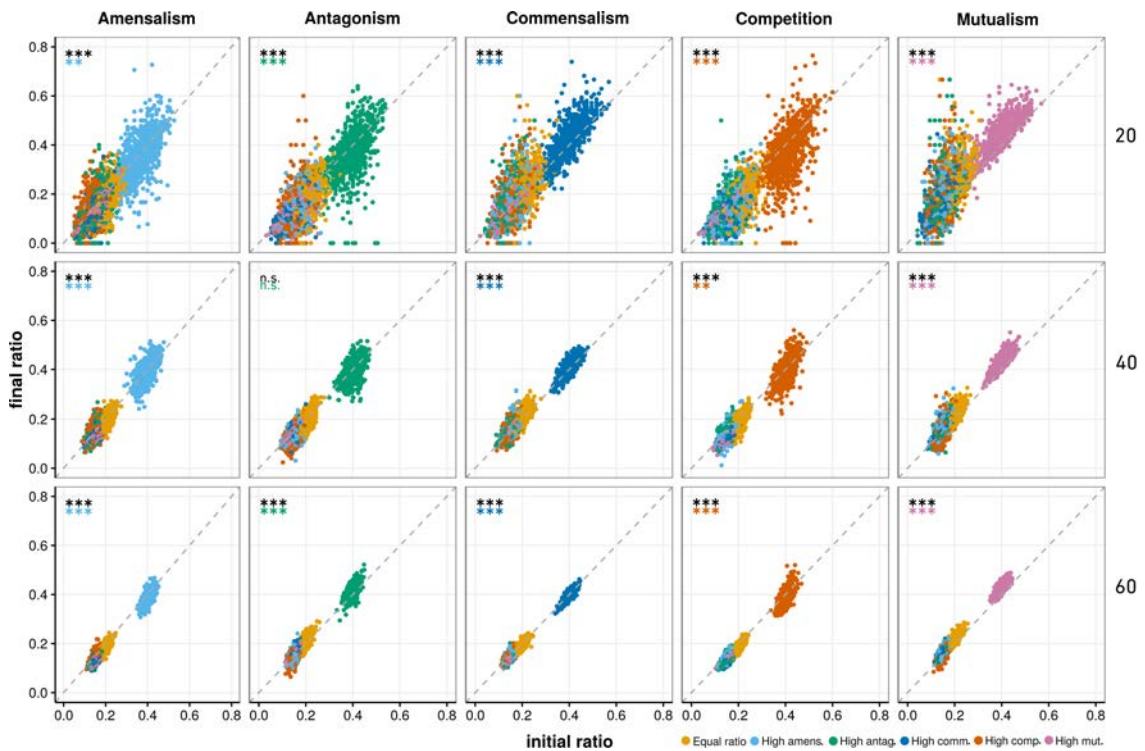
FIGURE 3.3: Initial and final frequency of each interaction type in each community parameterization (rows: richness levels, columns: interaction frequencies levels). Each dot represents a single simulation, color code is the same as Fig. 3.2. Upper left symbols in each panel represent the significance of the difference in initial and final ratios according to Wilcoxon signed rank paired tests, in black for the whole set of simulations, and colored for the simulations with high ratio of the respective type (n.s.: p-value ¿ 0.05, *: p-value < 0.05, **: p-value < 0.01, ***: p-value < 0.001. See Table A.3.2.3 for details.

Does our model reflect structural patterns observed in empirical networks?

Focusing on the structural features listed by Jacquet et al. (2016), we checked three features observed in empirical networks: the distribution of interaction strengths (species impacts in our scheme), their variation in magnitude with trophic level, and the correlation of antagonistic pairwise interaction impacts. The distribution of species impacts in our model communities ($I_{i,j}$ in Eq. 3.1) was positively skewed in all cases, with communities with high proportion of negative interactions being the most skewed (Fig. 3.4, Table A.3.2.4). The magnitude of species impact decreased consistently with increasing trophic level (Fig. 3.4, Table A.3.2.5 and Table A.3.2.6). Lastly, there was a significant negative correlation in the values of pairwise species impact for antagonistic interactions (Fig. 3.4, Wilcoxon signed-rank tests, $V = 0$, $p < 0.001$ in all cases).
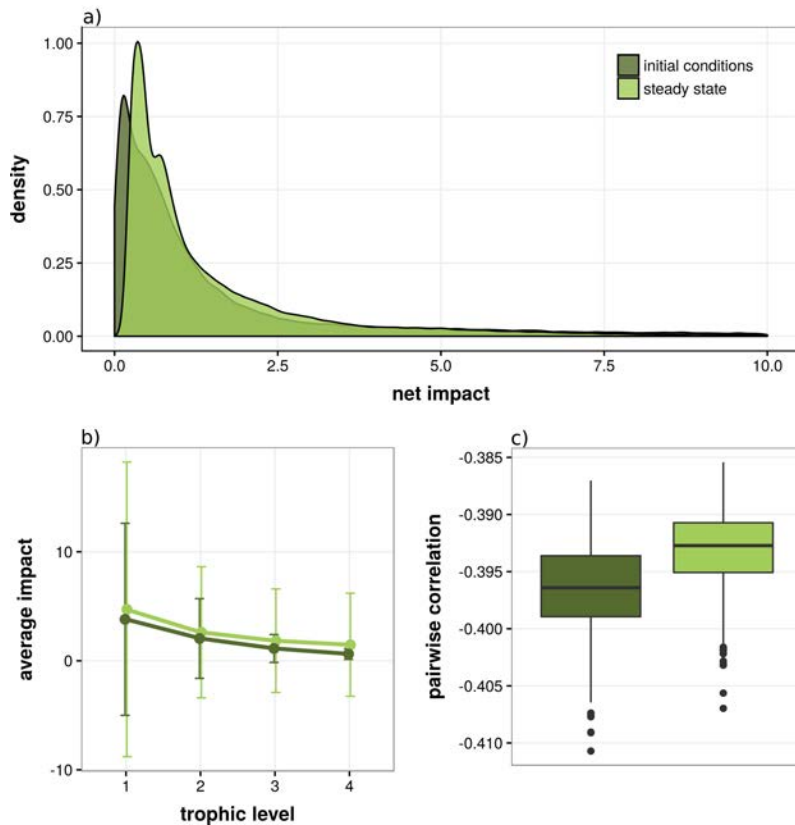
Figure 3.4: Structural patterns observed in our model, at the initial and final steps of the simulations. Data shown corresponds to simulations with an initial richness of 60 species and equal probability of occurrence for every interaction type. a) Skewed distribution of species impacts. b) Decrease in average impact per trophic level (error bars represent an interval of one standard deviation centered in the mean). c) Correlation of species impact among pairs of species. In this panel, the only interactions accounted for are antagonistic ones.

3.4 Discussion

Our simulations indicate, primarily, that positive interactions are key for maintaining species persistence, particularly in species-poor communities. For understanding the outcomes of our model and in order to place them in a general context, we first evaluate the role and implications of modeling interaction impacts based on species abundances and interaction frequencies. Secondly we analyze the combined influence of other community-level factors.

Species persistence and pairwise direct interactions

All other things being equal, the number of interactions every species has with other species (i.e., their degree) is expected to increase with increasing number of species in the community. This is exactly what we recorded in our model communities: by keeping network connectance constant, we obtained average degrees of 9.5 for communities of 20 species, and degrees of 19.5 and 29.5 for communities of 40 and 60 species, respectively (values not far from the empirical estimates obtained by Kéfi et al. (2015), who reported an overall connectance of

0.47 for a community of 104 species, and thus a mean overall degree of 24.2).
Given such a scenario, in species-poor communities the dynamics of a species will
directly depend on only a handful of pairwise interactions. In such cases, a single
interaction with high impact will have a disproportionate direct effect on species
dynamics and, by extension, the prevalence of negative or positive interaction
types will be an important driver of persistence at the community level.

The direct impact of interactions in communities is not only dependent on their
numbers, but also on the abundances of the interacting species. Considering a
skewed SAD (Species Abundance Distribution) of the overall community, as in our
main simulations, the percentage of rare species (e.g. these with < 10 individuals)
increases and then stabilizes with increasing richness, while the percentage of
very abundant species (e.g. with ¿ 100 individuals) decreases (Table A.3.2.7). In
species-poor communities, thus, a higher proportion of interactions will involve
very abundant species, increasing the probability of comparatively strong direct
impacts on species dynamics. As richness increases, more interactions will take
place between comparatively rare species. The average impact per interaction will
decrease accordingly (Fig. A.3.2.2), with the effect that average persistence will
increase regardless of the distribution of interaction types.

An important consequence of the differential effect of interaction types on
species persistence is that species engaging in a high number of direct positive
interactions will tend to persist and maintain their interactions, whereas species
with a high number of direct negative interactions will tend to go extinct more
frequently and, thus, their associated interactions will be lost, increasing the over-
all ratio of positive interactions (Fig. 3.3). This reasoning is, however, contingent
on the modeling assumption that there is no interaction rewiring. Keeping in
mind this strong assumption, if these results hold, natural assemblages should
be filtered to maintain a relatively high ratio of direct positive interactions, in
particular in species-poor communities, and species with a high degree of nega-
tive interactions will be rare and, in any case, have otherwise strong life-history
traits that allow them to persist. Note that, throughout the study, we limit our
discussion to the role of direct interactions. The importance of indirect or net
effects for understanding community patterns is well established (e.g. Montoya
et al. 2009), and the mechanisms proposed here for linking species interactions,
abundance and persistence, would be improved by accounting for the role of
these higher-order effects. However, in model networks, net effects are commonly
analyzed by calculating the negative of the inverse Jacobian matrix (Novak et al.,
2016). The formulation of our model, without static interaction coefficients and,
potentially without attaining static equilibria, limits the applicability of analyses
based on Jacobian matrices. Therefore, we opted not for calculating net effects
and leave their analyses in our framework for future studies.

By explicitly modeling species impacts based on species abundances and in-
teraction frequencies, our interpretation of species persistence and community
dynamics differs fundamentally from that of other theoretical models of multiple
interactions (e.g. Mougi and Kondoh 2012). Furthermore, our response factor,
species persistence, also differs from the common local stability analyses per-
formed in the majority of theoretical network studies. Despite these fundamental
differences, some common trends seem to surface. Much like our finding that the

frequency of interaction types is less important in speciose communities, in the study by Mougi and Kondoh (2012) increasing richness allowed for high local stability regardless of the proportion of positive to negative interactions (but see Suweis et al. 2014). With a completely different methodology, built on individual-based models, Lurgi et al. (2016) further found that increasing the proportion of mutualistic links increased overall stability in their model. Yet another, more general interaction model showed that positive interactions tend to become dominant in interaction networks as a consequence of spontaneous self-organization (Jain and Krishna, 2001). Overall, these independent lines of evidence point to the combined importance of positive interactions and community size on stability patterns in a broad sense.

The relationship between species richness, abundances and interaction types may shed light on other general questions in community ecology, aside from the comparison with previous theoretical models.

First, in line with empirical findings from plant communities in stressful environments (Soliveres and Maestre, 2014; Cavieres and Badano, 2009), we have shown that a high ratio of positive to negative interactions significantly increases species persistence, particularly in communities with low initial richness. By the explicit consideration of four discrete trophic levels, we show that a preponderance of positive interactions is particularly important for the persistence of intermediate consumers (Fig. A.3.2.1), upper panels). These species are preyed upon by top predators and also subject to competition (both direct as modeled and indirect as a result of resource consumption) and amensalism. Hence, they are potentially the most benefited from engaging in mutualisms with species from adjacent trophic levels. As mutualistic interactions are most prevalent across adjacent trophic levels (Fig. 3.1), intermediate species will be the ones showing a highest degree of these positive interactions. Note that we did not model competition for resources at the basal trophic level, and all our communities included a fourth trophic level of top predators. Thus, these latter species, not subject to predation (aside from a very small probability of intraguild predation, Fig. 3.1), are likely to have a strong top-down influence on the persistence of intermediate species.

Second, our findings contribute to reframing the debate on whether pairwise interactions are stronger in richer communities. On the one hand, the hypothesis of a gradient on pairwise interaction strength with latitude has been generally supported on empirical grounds (Schemske et al. 2009, but see Moles and Ollerton 2016), but it is unclear whether or how this pattern is affected by the richness of the analyzed communities. On the other hand, we have shown that if interaction impacts are neutral (i.e. driven solely by species abundances), then species impact will generally decrease with increasing richness. This theoretical result has been partially supported in a recent study that found that, on islands whose size granted a certain environmental stability, the strength of competitive and antagonistic interactions decreased with island size and richness (Schoener et al., 2016). Clearly, an array of factors can cause deviations from neutrality in interaction strengths (IS function in eq. 3.1), and hence the neutral interactions hypothesis should be viewed as a baseline for estimating species impacts when no other information is available. Such neutral estimations have already been applied for plant-pollinator

networks (Vázquez et al., 2012) or in sampling campaigns of multiple interactions networks (Pocock et al., 2012).

Emerging community structure further enhances persistence

Components of community structure, such as species diversity or different network-level metrics, have been regarded as key factors in previous modeling studies (Sauve et al., 2014, 2016), where accounting for empirically informed values generally enhances stability metrics. Such theoretical results are, however, difficult to validate, since empirical data on communities with varying structural patterns is extremely scarce. As an alternative for testing the adequacy of our model, we analyzed whether our model communities displayed properties comparable to those found in empirical networks. Recently, Jacquet et al. (2016) showed that empirical food webs possess three structural characteristics that clearly differentiate them from random counterparts: first, they display the classic skewed distribution of interaction strengths, whereby there are very few strong interactions and a majority of weak ones (McCann et al., 1998). Secondly, empirical food webs show strong pairwise correlations in interaction strengths, in line with theoretical findings (Tang et al., 2014). Thirdly, interaction strengths are not evenly distributed across trophic levels; rather, average interaction strength tends to decrease with trophic level. In our model, the skewed distribution of species impacts and their "pyramidal" arrangement are observed and maintained throughout the community dynamics (Fig. 3.4, panels A and B). On the other hand, the pairwise correlations generated in our model communities (Fig. 3.4, panel C) are significantly different from zero but smaller than those reported by Tang et al. (2014). Such disparity may be due to the lack of trait-matching mechanisms in our model, as trait-matching may give rise to increasingly specialized and correlated pairwise interactions (Santamaría and Rodríguez-Gironés, 2007).

The three patterns outlined by Jacquet et al. (2016), i.e. skewed distribution of impacts, pairwise correlations in interaction strength, and decrease of species impacts with increasing trophic level, are already present at the beginning of the simulations (Fig. 3.4), so they arise from the structural constraints of our community assembly process. It is therefore informative to analyze the dynamics of the model without these constraints, namely 1) a skewed Species Abundance Distribution of the overall community, 2) a sublinear scaling of overall abundances with increasing trophic level, and 3) a non-random distribution of links across trophic levels, for each interaction type (Fig. 3.1).

Relaxing these constraints does not modify the main qualitative patterns of our results, i.e. positive interactions and, to a lesser extent, increasing richness, have a positive effect on persistence (Fig. A.3.3.1), but quantitative outcomes vary. The effect of removing the second and third constraints on species persistence is negative, while removing the first constraint has a generally positive effect on persistence. This effect is particularly strong for upper trophic levels, where average persistence varies widely depending on the assembly constraints imposed (Fig. A.3.3.2). These results invite the interpretation that community structure, both in terms of the topology of the different interaction types and the distribution of species abundances across trophic levels, is a key factor for maintaining high

levels of persistence. Despite their recorded importance, understanding of these factors in empirical communities is still limited. Further empirical work is needed to evaluate the generality of the abundance scaling law (Hatton et al., 2015) for multiple trophic levels and community types, and, importantly, to understand its underlying mechanisms. Regarding the distribution of interaction types, our approach was to assign probabilities of occurrence based in empirical observations. This methodology is biased towards the most studied interaction types (antagonism, competition and mutualism), and towards easily observed organisms and interactions, thereby failing to account for functionally important yet rarely considered organisms, such as microorganisms, parasites or parasitoids. It has been shown, for example, that accounting for parasites when analyzing food webs significantly modifies network structural patterns (Lafferty et al., 2006), so the interaction probabilities obtained here should be taken as broad estimates. Despite these shortcomings, evidence is increasing theoretically and empirically that link topology is key not only for consumer-resource, but for all interaction types (Pocock et al., 2012; Evans et al., 2013; Kéfi et al., 2015, 2016; Sauve et al., 2016). Due to the difficulty in obtaining reliable estimates of multiple interactions at once in empirical communities (García-Callejas et al., 2018*b*), we currently do not know whether the distribution and topology of interaction types is homogeneous across communities or how it is influenced by habitat type or environmental factors.

The significant variation in persistence ratios with structural patterns shown here suggests that theoretical studies relying on idealized communities (e.g. totally mixed interactions and/or random distributions of biomass across trophic guilds) are likely to miss key mechanisms for maintaining species persistence. Rather, future studies on multiple interactions networks should take into account the variability of community-level factors present in natural assemblages, like interaction frequencies and distribution, or abundance scalings across trophic levels. Our model is a first step in that direction, but it is important to note that the insights obtained are, of course, contingent on the assumptions made. In particular, important features of the model are the constant connectance hypothesis and the implementation of dynamic interaction impacts. Furthermore, we assumed that the degree of a species is independent of its relative abundance in the community. While none of these assumptions hold completely true in nature, they represent convenient starting hypotheses for modeling complex ecological communities, because ecological interpretations can be drawn when empirical systems deviate from these assumptions (Banašek-Richter et al., 2009). Further investigation on the differential functional form of the different interaction types, e.g. as outlined for mutualism by Holland et al. (2002), and on interaction rewiring (Valdovinos et al., 2010; Mougi, 2016*b*), will also help refine the conclusions obtained here. Aside from these potential developments, our results can be used to establish baseline predictions on the dynamics of natural communities across gradients of richness or other factors. In that regard, the sensitivity of species-poor communities to interaction diversity is of particular interest: as these communities are particularly endangered by anthropogenic drivers of ecosystem change (Cavieres and Badano, 2009), it is paramount to evaluate this theoretical result and its potential consequences for management and conservation schemes.

3.5 Conclusions

To understand how the persistence of species is influenced by the complex networks of interactions in which they are inserted, it is important to develop models that account for the diversity of interactions present in nature, and that incorporate realistic constraints to the structure of these networks. By developing one of such models, we found that species' local persistence is not explained by a single axis of variation in network properties, but rather is contingent on the interaction of several structural factors: the diversity and distribution of biotic interactions, the size of the community, and the distribution of species abundances across trophic levels. In particular, we found that a high prevalence of positive interactions can lead to increased persistence of species in communities with low richness, whereas speciose communities can sustain varying ratios of interaction types without significant decreases in average persistence. Although simulation studies are, by definition, affected by a number of simplifying assumptions, we found that our simulated networks have emerging features also present in empirical networks, suggesting that our modeling framework captures part of the mechanisms that maintain the richness and diversity of natural assemblages. The insights from network models, such as ours, are one of the complementary ways in which ecologists approach the understanding of local species persistence, and should prove valuable in developing a robust predictive framework for its variation across different types of gradients.

On the variability of Species Abundance Distributions with trophic guild and community structure 4

Abstract

Species Abundance Distributions (SADs) are one of the strongest generalizations in community ecology, but their variation across trophic levels remains largely unexplored. I study the variation in SAD metrics across trophic guilds in model and empirical communities. First, I use a theoretical model that allows tracking the variations in abundances across trophic levels, accounting for variations in species richness and network connectance. Second, I compare the empirical SADs of 226 terrestrial plant communities and 497 mammal communities comprising species grouped in three general trophic guilds (herbivores, omnivores, and carnivores). I analyze the differences in evenness and skewness of the empirical SADs across the different trophic guilds, controlling for species richness, spatial and temporal resolution of the sampling. In model communities, evenness is highest for herbivores, and decreases in omnivore and carnivore guilds. The richness and connectance of the community network are also negatively correlated with guild evenness. In empirical datasets, plant communities are significantly less even and more skewed than mammal ones. There are no significant differences in SAD metrics between the different mammal guilds, but carnivores are comparatively rare (i.e. have a higher proportion of species than individuals), whereas omnivores are comparatively more common. Species richness has a positive effect on both evenness and skewness, and spatial and temporal extent have negative effects on evenness and do not affect skewness. I argue that the difference between plant and mammal guilds can be related to higher niche availability in animals than in plants, that decreases the importance of competitive exclusion in mammal guilds. As no systematic differences were found between the SADs of mammal herbivores, omnivores, and carnivores, this may indicate similar niche availability, when averaged across habitat types, for the different animal trophic guilds.

4.1 Introduction

Most species, in any ecological community, are comparatively rare, and only a few of them are very abundant. This empirical observation is one of the few true universal laws in ecology, a pattern that is observed in all kinds of communities and guilds, from small arthropods (Basset and Kitching, 1991) to tropical trees (He et al., 1997). The Species Abundance Distribution (SAD) describes precisely this variation in species abundances within a given assemblage.

The information contained in SADs, aside from its theoretical interest in understanding community dynamics (Hillebrand et al., 2008), can be of interest for conservation and management (Matthews and Whittaker, 2015) or for estimating ecosystem functions such as primary productivity (Wilsey and Potvin, 2000). It is therefore important to understand which are the main axes of variability in SAD shape across guilds, and what are the ecological processes underlying this variability. So far, important efforts have been devoted to understand variation in species abundances across enviromental gradients (Ulrich et al., 2016; Passy, 2016), levels of disturbance (Komonen and Elo, 2017), spatiotemporal scales (Borda-de-Água et al., 2012), or multiple factors combined (Arellano et al., 2017). Intrinsic dif-

ferences in species-level traits among the species that make up the community will also be reflected in the SAD. For example, core and satellite species of an ecosystem are likely to differ in their intrinsic abundances regardless of other factors (Magurran and Henderson, 2003), and the degree of trophic or habitat specialization of different species may also be related to their relative abundances (Labra et al., 2005; Matthews and Whittaker, 2015).

Despite these many advances, in the debates on the mechanisms that shape SADs, virtually all theories and hypothesis that relate SAD shape to ecological processes at the local scale refer to horizontal communities, i.e. communities of a single trophic level. Thus, these theories emphasize the role of either neutral dispersal and drift (Hubbell, 2001) or horizontal selection (Vellend, 2016). But natural communities form a complex network of species linked by different types of biotic interactions both horizontally (within a given trophic guild) and vertically (across trophic guilds, Fig. 4.1). The influence of the interaction topology on the abundance patterns of the different guilds of a community has, to my knowledge, never been explored systematically.
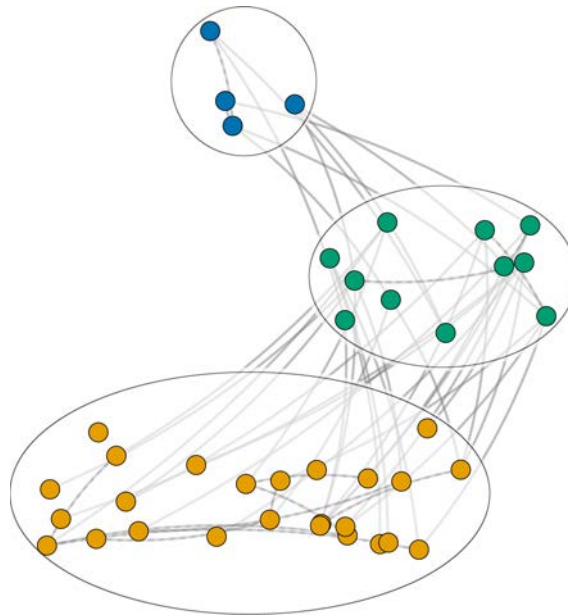
FIGURE 4.1: A schematic ecological community with three disjoint trophic guilds. The areas within the ellipses represent the domain of horizontal community ecology that is the subject of most SAD studies, focusing on intra-guild interactions (dashed grey lines) and assuming that interactions with other guilds (full grey lines) are negligible. In this study, I focus on how interactions across guilds drive variations in SAD metrics.

In complex, multitrophic ecological communities, trophic guilds (sensu Fauth et al. 1996) differ in fundamental properties that can potentially be reflected in their associated abundace distributions. First, several studies have demonstrated that basic descriptors, such as biomass or species richness, vary predictably with trophic level. For example, richness pyramids have been shown to be widespread in empirical food webs from different ecosystem and taxonomic types, particularly in marine habitats (Turney and Buddle, 2016). Another distribution, that of biomass across trophic guilds, also has a long history in ecology, starting with the

seminal studies by Lindeman (1942) or Odum (1957). Focusing on the relationship between two adjacent trophic levels, Hatton et al. (2015) showed that the biomass of empirical guilds of herbivores and their associated predators scales generally with a power-law of exponent 3/4. They also showed that, in their data, the relationship between mean body mass and community biomass is non-significant for most of the functional groups they studied. As such, if body mass varies in a similar fashion in different trophic levels, the scaling in biomass should also be reflected in a scaling on number of individuals at each trophic level, as foretold by Ramón Margalef (1980).

Other patterns associated to the distribution of abundances, such as species rarity or the degree of dominance, can potentially vary across different trophic guilds, but empirical evidence is scarce. In a study of macroinvertebrate communities, predators showed a higher proportion of species than of individuals in the overall community (Spencer, 2000), pointing to a higher rarity in predator species. Furthermore, Spencer (2000) showed that predator and non-predator species did not vary significantly in the ratios of dominance of the most abundant species. More recently, Dornelas et al. (2011) showed that relative dominance decreased consistently with increasing richness in communities of freshwater fish.

Overall, these lines of evidence suggest a complex, combined influence of the richness and trophic position of a guild on its abundance patterns. In a first approximation, the number of different resources available to a given trophic guild and the partition of these resources among its constituent species (Tokeshi, 1990; Sugihara et al., 2003) will ultimately drive the guild's SAD. As the trophic interactions among guilds are encoded in the topological structure of the community food web, this structure is likely to play a role in modulating SAD variability across guilds.

Analyzing abundance distributions in communities comprising several trophic guilds is complicated further by a number of factors. For example, movement capacity generally increases with trophic position (McCann et al., 2005), and in turn, it significantly influences SADs and their variation with sampled area (Borda-de-Água et al., 2017). Therefore, different trophic guilds in the same community will likely require varying sampling areas in order to obtain their abundance patterns in a consistent fashion (see also Holt et al. 1999). Another issue that needs to be considered when comparing trophic guilds of different communities is precisely how to divide species among guilds in a general way. Broad categories such as herbivores/omnivores/carnivores provide groupings applicable to communities of different ecosystem types, but are likely to be too general, lumping together species with very different ecologies. On the other hand, clearly defined guilds for a given community type (e.g. sap-feeding insects in salt marsh grasses) will be too specific to allow comparisons with guilds from other ecosystem types. Therefore, a robust analysis of the role of trophic guild in SAD metrics needs to control for (1) the variations in richness across guilds, (2) the spatial and temporal extent of the data collection, and (3) the process of defining trophic guilds in a general and informative way.

Here I approach the general question of whether SAD metrics vary predictably across trophic guilds, in two complementary ways. First, I combine a model of food web structure with niche apportionment schemes for studying how SADs of

different trophic guilds vary in model communities with varying network structures. Second, I analyze SAD patterns of two well-resolved datasets on community abundances of plants (Phillips and Miller, 2002) and mammals (Thibault et al., 2011). I compare SAD patterns of plant communities and three mammal trophic guilds, controlling for guild richness, spatial and temporal extent of the data collection.

4.2 Methods

The relationship between SAD properties and trophic guild: A theoretical model

Analyses of species abundance distributions are based, on their first stage, on the grouping of species that are supposed to share certain properties of interest, such as taxonomic relatedness, spatial location or resource use (Fauth et al., 1996). As a starting point, I focus on the role of the different trophic guilds in a local multi-trophic community. Intuitively, the variability in number of individuals between species of a given trophic guild will depend on inter-specific variation in both species-level traits and resource use. Assuming, as a working hypothesis, that the main difference between species within a guild is in their competitive ability to acquire resources, it can be hypothesized that the degree of resource overlap between the species will play an important role in determining their variations in abundance (Sugihara et al., 2003).

This intuitive, qualitative hypothesis can be more precisely formulated by combining models of network structure and resource partitioning schemes. Consider a single herbivore that is preyed upon by a number of predators. All else being equal, the partition of the prey resource will be driven by the competitive ability of these predators, and will be reflected in their own abundances (an energetic view of abundance, Isaac et al. 2013). When an arbitrary number of resources can be exploted by the species of the trophic guild, the specialization level of the species will influence the degree of exploitative competition between the guild's species, and indirectly its distribution of abundances. In network terminology, the level of specialization of a species is given by its degree, the number of interactions in which it engages, and indirectly, by the connectance of the network, the ratio of realized to potential interactions in it.

For testing the expectation that abundance distributions will vary with the level of specialization of the trophic guilds, and thus with network connectance, I generated food webs with varying connectance and richness values. Then, I grouped their constituent species in trophic guilds, calculated the expected abundances of each species according to a resource apportionment model, and compared the resulting distribution of abundances of the different guilds. There is a long tradition of resource partitioning models along a single axis, and here I implemented the Random Fraction model, which has been shown to fit empirical datasets reasonably well (Tokeshi, 1990). In this scheme, the resource is divided sequentially into fractions, until each consumer is given a fraction of the available resource. At each step, the fraction that is divided is randomly chosen, so that ei-

ther the biggest fraction could be divided, leading to more equitable distributions, or the smallest fraction, leading to a bigger share for a single species. This scheme generates dominance hierarchies intermediate between a purely *dominance pre-emption* scheme, in which dominant species always gets the higher share of the resource, and a *dominance decay* scheme, in which resources are distributed most equitably (Tokeshi, 1990).

Food webs were generated using a modified version of the niche model (Williams and Martinez, 2000). The original niche model takes a single niche axis in which all species are placed to generate trophic links allowing for a certain degree of intraguild predation (the original formulation is given in Williams and Martinez 2000, and its particularities with respect to other food web models are explored, for example, in Dunne 2006). The network topologies generated with it are similar in terms of goodness-of-fit to those from more complex models (Williams and Martinez, 2008), so it remains an appropriate model for generating food web structures in the absence of detailed information on trait structure (Gravel et al., 2016*a*). One of its limitations, however, is the systematic underestimation of the proportion of primary producers and herbivores compared to empirical food webs. In this study, I imposed a minimum fraction of 0.2 of primary producers in the generated food webs. Furthermore, I removed all directed cycles from the web, in order to make the propagation of biomass across species feasible. For each cycle (i.e. a series of nodes and links that eventually form a closed chain), I selected one of its constituent links randomly and assigned the resource to be a basal species. These two modifications to the original model are likely to modify some emergent properties of the network structure, but the resulting connectance of the generated food webs is maintained, and the proportion of primary producers and herbivores is increased with respect to the original formulation. I grouped the species in primary producers, herbivores (i.e. species whose only feeding sources are primary producers), omnivores (species that feed in both primary producers and other species), and carnivores (species that do not feed on primary producers).

In order to obtain the abundances of the species in the food web, the abundances of the basal species need to be specified beforehand, as this model represents a static bottom-up approach. I generated basal abundances from a Weibull distribution with scale = 4.7 and shape = (0.15,0.2), derived as the average best fit from the 226 sites of the GENTRY dataset (see *datasets* section).

I considered three levels of species richness (50, 100, and 200 species), and three levels of network connectance (0.1, 0.2, and 0.3). For each combination of richness and connectance, I generated 1000 networks and quantified the evenness and skewness of the SAD of the different trophic guilds (see next section).

I analyzed the variability of SAD metrics with connectance, species richness and trophic guild by using regression models. In particular, I used linear mixed-effect models (R package "lme4", Bates et al. 2015) with richness, connectance, and trophic guild as fixed effects, and replicate (e.g. the 1000 simulated networks for each combination of richness and connectance) as a random effect. As I am not interested in predictions from this model, but rather in the effect of the different predictors, I did not perform model selection procedures.

Metrics for quantifying Species Abundance Distributions

Methodologically, the comparison of SADs is still an unresolved problem in community ecology: there is no standard method for comparing SAD shape of guilds with arbitrary numbers of species or individuals, with most comparisons being qualitative (McGill et al., 2007) or being made between relatively similar communities that don't differ much in richness or size (e.g. samples from polluted and unpolluted habitats, Matthews and Whittaker 2015). In order to assess the variability between SADs in a general way, robust metrics need to be developed that are independent of number of species and individuals, i.e. that reflect solely the variability in the shape of the distribution. In this study, I assess the variability in SAD shape through two complementary metrics, that quantify the evenness and the skewness of the distribution.

Evenness is defined after the "Hill number" of species diversity, also known as the effective number of species (Jost, 2006). This diversity metric represents how many equally-abundant species would give the observed mean proportional species abundance (Tuomisto, 2012). The evenness metric derived from the effective number of species has a series of desirable properties, summarized in Smith and Wilson (1996). It is also conceptually similar to the variance of a distribution, but the evenness metric has the advantage of having a clear ecological meaning. The skewness metric is simply a robust version of the third moment of a statistical distribution (Brys et al., 2004). Throughout this study, I apply these metrics to the natural abundances of both the simulated and compiled data.

Empirical SAD patterns across trophic guilds

Datasets

I analysed two datasets that report species abundances at different sites along with the spatial and temporal effort from each site. Gentry's Forest Transect Dataset (GENTRY, Phillips and Miller 2002) compiles observations from 226 sites of 0.1 ha in temperate and tropical forests across the globe. At each site, Gentry and collaborators collected the abundance of all plant species with stem diameters at breast height equal to or exceeding 2.5 cm. The second dataset is the Mammal Community Database (MCDB, Thibault et al. 2011), which provides abundances of 660 mammal species in 940 sites, alongside detailed information about the sampling and context of the local community. Rank-abundance curves of one GENTRY site and four MCDB sites are shown in Fig. 4.2.

Another global dataset on mammal foraging habits (Wilman et al., 2014) was used to derive trophic guild categorizations for every species in the MCDB dataset. I assigned each species to one among three general trophic guilds: (1) herbivores (including folivores, granivores, frugivores, and nectarivores); (2) omnivores, and (3) carnivores (feeding on invertebrates, vertebrates, fish, and carrion). Herbivores and carnivores are species that have at least a 70% of their diet from plant or animal origin, respectively, and species whose diet is < 70% herbivore or carnivore are labelled omnivores. While more detailed trophic guild distinctions are possible, the representativeness of the different categories varies drastically (e.g. there are only 22 mainly frugi/nectarivore species versus 324

foli/granivore ones). In a basic categorization such as the one presented here, the three trophic guilds are well represented (374 herbivores, 145 omnivores, 179 carnivores).
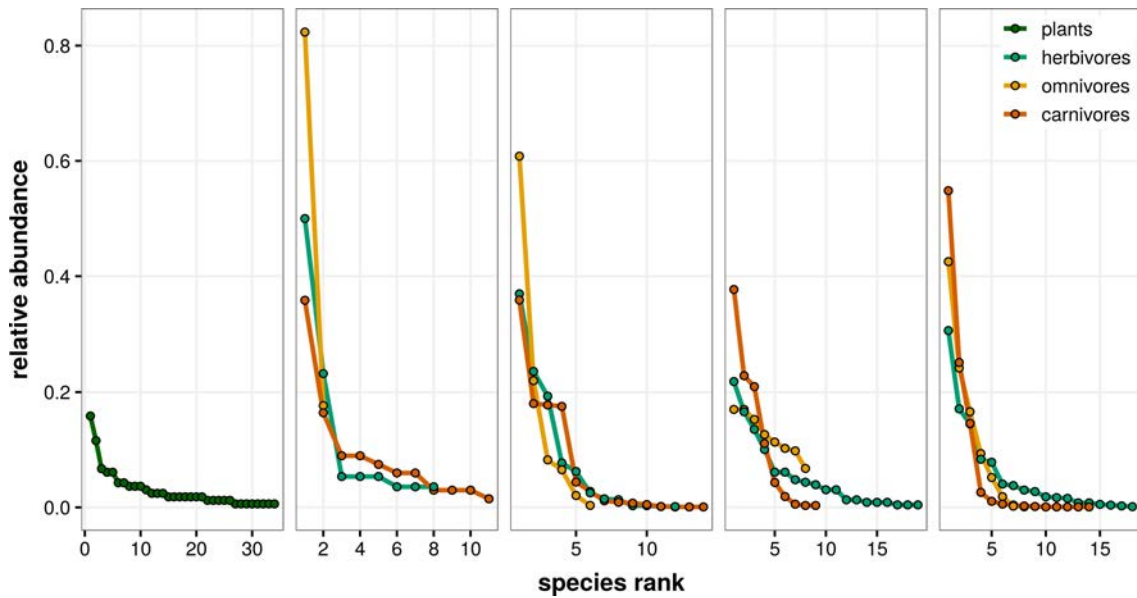
Figure 4.2: Rank-abundance curves for five sites of the empirical datasets. The leftmost panel shows a curve from a GENTRY site, the other four are sampling sites of the MCDB dataset.

Statistical analyses

I calculated the evenness and skewness metrics of each guild at sites in which there are at least three species of that guild, in order to avoid potential biases (for example, a guild of a single species is completely even, or a guild of two species is never skewed). The variation of the SAD metrics with trophic guild was analyzed via statistical models. Evenness values are bounded within the interval [0,1], so a beta regression is an appropriate choice for modelling such bounded data, given the flexibility of the beta distribution. I transformed the evenness values in order to obtain data without proper zeroes and ones, i.e. bounded in (0,1), following Smithson and Verkuilen (2006), and applied a beta regression with trophic guild, species richness, temporal extent and spatial extent as predictors. In particular, I used the R implementation of the GAMLSS family of models (Rigby and Stasinopoulos, 2005), which allows probability density functions to be specified by any number of parameters, themselves functions of the independent variables. I modelled the evenness probability density function with two parameters μ and σ, named the *location* and *scale* parameters. These parameters are related to the parameterization of the beta distribution in terms of two shape parameters α and β in the following way:

$$\mu = \frac{\alpha}{\alpha + \beta} \tag{4.1}$$

$$\sigma = \frac{1}{\alpha + \beta + 1} \tag{4.2}$$

The mean and variance of the beta distribution in terms of μ and σ is:

$$\hat{y} = \mu \tag{4.3}$$

$$var = \sigma^2 * \mu * (1 - \mu) \tag{4.4}$$

For the final model, I selected the link functions of μ and σ, and the final set of predictors, via AIC model selection.

Skewness presented a clearly bimodal distribution, with peaks at 0 and 1. Due to the difficulty of modelling such continuous bimodal data, I opted for categorizing the response into three levels of skewness: highly negative, low skewness, and highly positive, represented by the intervals [-1,-0.5), [-0.5,0.5], and (0.5,1]. This response was modelled via a multinomial regression with the same set of predictors as the evenness metric, and AIC model selection was also performed to obtain the final set of predictors.

For the MCDB dataset, it is common to observe species from two or more trophic guilds at the same site (Fig. 4.2). It is therefore possible to calculate the rarity of each guild as the difference between its proportion of individuals and its proportion of species in the local communities (Spencer, 2000). Furthermore, to complement this calculation, I obtained the relative dominance value of each guild at each site, measured as the abundance of the most abundant species divided by the summed abundances of its guild (Spencer, 2000; Dornelas et al., 2011).

4.3 Results

Theoretical model

Evenness and skewness metrics show contrasting responses to variations in trophic guild, richness and connectance (Tables 4.1 and 4.2, see Fig. 4.3 for a subset of the results). After a high increase in evenness from primary producers to herbivores, the metric decreases on average with trophic guild. Likewise, richness displays a negative relationship with evennes, whereas connectance shows a more complex relationship, with minimum overall evenness observed at intermediate levels of connectance (Table 4.1). Skewness, in turn, displays almost opposite trends: it increases with increasing trophic position, richness, and connectance (Table 4.2).
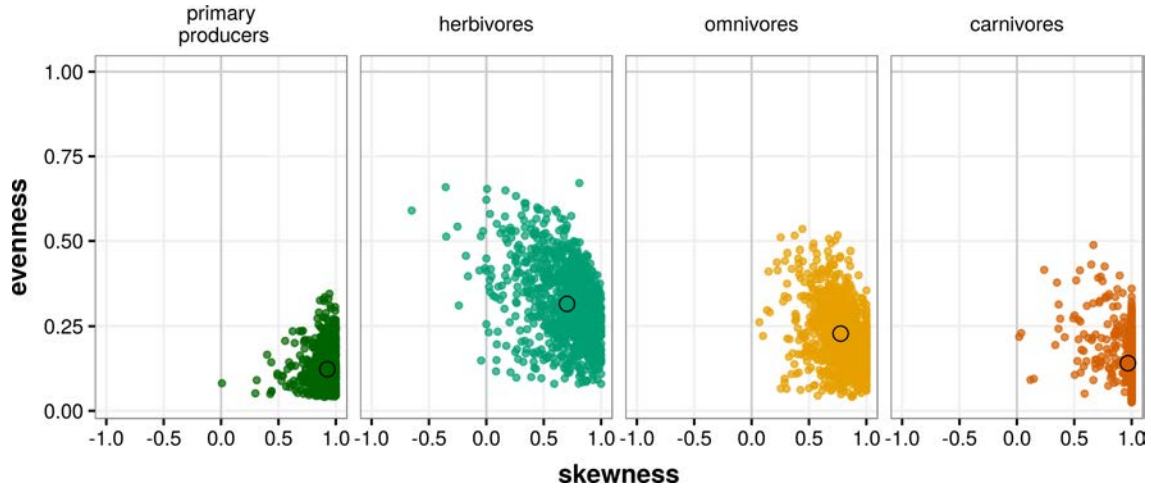
Figure 4.3: Evenness and skewness values for the trophic guilds of simulated networks. In this figure, each dot represents one realization of a network with richness = 100 and connectance = 0.2. Note that the abundances predicted by the model correspond to the three consumer levels, whereas abundances of primary producers are inputs to the model, and are shown for reference. Black circles represent the centroid of the two-dimensional distributions.

Table 4.1: Estimated regression parameters, standard errors, t-statistic values and p-values for the mixed effect model *evenness ~ richness + connectance + trophic guild + random(replicate)* of the theoretical model. $\sigma_{replicate}$ is $5.3 * 10^{-8}$, and the r^2 of the model is 0.4

Variable	Estimate	Std. Error	df	t value	p-value
(Intercept)	0.41	$1.848 * 10^{-3}$	$2.63 * 10^4$	221.871	< 0.05
richness-100	-0.091	$1.72 * 10^{-3}$	$2.63 * 10^4$	-53.237	< 0.05
richness-200	-0.155	$1.72 * 10^{-3}$	$2.63 * 10^4$	-89.997	< 0.05
connectance-0.2	-0.007	$1.7 * 10^{-3}$	$2.63 * 10^4$	-4.351	< 0.05
connectance-0.3	0.007	$1.73 * 10^{-3}$	$2.63 * 10^4$	3.773	< 0.05
trophic.guild-omnivores	-0.079	$1.7 * 10^{-3}$	$2.63 * 10^4$	-46.453	< 0.05
trophic.guild-carnivores	-0.167	$1.73 * 10^{-3}$	$2.63 * 10^4$	-96.437	< 0.05

Table 4.2: Estimated regression parameters, standard errors, t-statistic values and p-values for the mixed-effects model *skewness ~ richness + connectance + trophic guild + random(replicate)* of the theoretical model. $\sigma_{replicate}$ is 0.0032, and the r^2 of the model is 0.24

Variable	Estimate	Std. Error	df	t value	p-value
(Intercept)	0.561	$3.65 * 10^{-3}$	$1.9 * 10^4$	153.603	< 0.05
richness-100	0.117	$3.39 * 10^{-3}$	$2.5 * 10^4$	34.574	< 0.05
richness-200	0.177	$3.4 * 10^{-3}$	$2.5 * 10^4$	51.957	< 0.05
connectance-0.2	0.019	$3.36 * 10^{-3}$	$2.53 * 10^4$	5.674	< 0.05
connectance-0.3	0.0048	$3.42 * 10^{-3}$	$2.53 * 10^4$	1.414	0.157
trophic.guild-omnivores	0.086	$3.36 * 10^{-3}$	$2.53 * 10^4$	25.739	< 0.05
trophic.guild-carnivores	0.253	$3.43 * 10^{-3}$	$2.54 * 10^4$	73.909	< 0.05

Empirical datasets

The statistical model for evenness included all the original predictors (trophic guild, richness, spatial extent and temporal extent, Table 4.3). Plant guilds were

the less even ones overall, showing significant differences with all other guilds (panel (a) of Fig. 4.4, Table A.4.1.1). Among mammal guilds, herbivores show the highest average evenness, after which it further decreases with increasing trophic rank, although the differences are non-significant (Table A.4.1.1). This overall pattern of a significant increase from primary producers to consumers followed by a sustained decrease is qualitatively similar to the patterns obtained with the theoretical model, although the evenness values of the theoretical model are much lower than those of the empirical datasets (compare Figs. 4.3 and 4.4). Richness has a positive effect on evenness, while also decreasing its variability (compare the sign of μ and σ richness parameters), whereas increasing temporal and spatial extent has a negative effect on mean evenness, and no effect on its variability (Table 4.3).
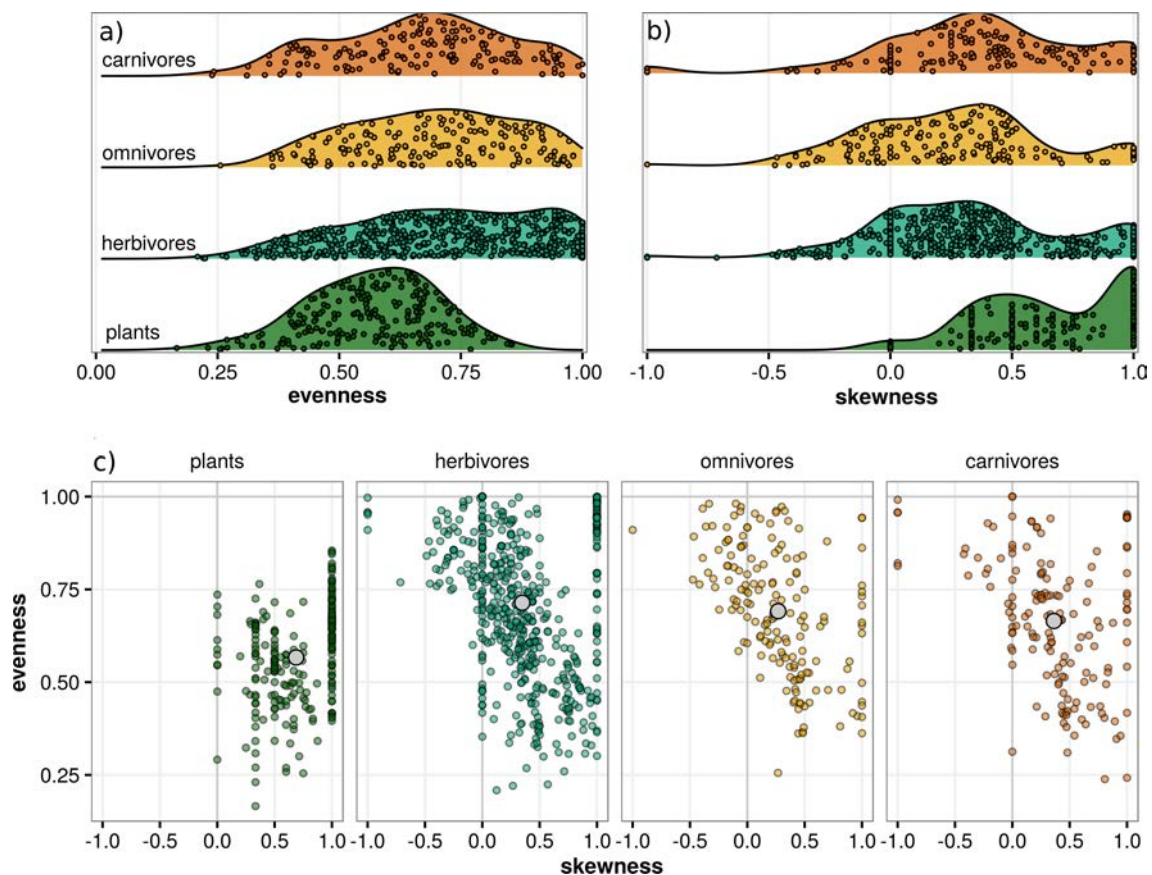
FIGURE 4.4: Density distributions of evenness (a) and skewness (b) values of the guilds studied, and the combined distribution of both metrics (panel c, cf. the theoretical results of Fig 4.3).

The final model for skewness included trophic guild and richness as the only predictors. Again, there were significant differences between plant and mammal guilds in their average skewness (Table 4.4). Plant and mammal guilds were different mainly when considering low and positive skewness levels, where plants showed the highest average skewness, followed by a drop in all mammal guilds, which showed no statistical differences (Fig. 4.4, Table A.4.1.2). Again, a similar qualitative trend is observed in the theoretical model (Fig. 4.3). The effect of

Table 4.3: statistical model coefficients for the evenness of the empirical datasets. See the main text for explanation of the μ and σ parameters. The r^2 of the overall model is 0.39

Variable	Estimate	Std. Error	t value	p-value
μ link function: cloglog				
(Intercept)	-0.509	0.039	-12.824	< 0.05
trophic.guild-herbivores	0.8681	0.055	15.882	< 0.05
trophic.guild-omnivores	0.753	0.062	11.975	< 0.05
trophic.guild-carnivores	0.711	0.069	10.382	< 0.05
spatial.extent	$-7.8 * 10^{-7}$	$3.1 * 10^{-7}$	-2.481	< 0.05
temporal.extent	$-3.8 * 10^{-3}$	$1.3 * 10^{-3}$	-2.914	< 0.05
richness	$3.2 * 10^{-3}$	$2.6 * 10^{-4}$	12.126	< 0.05
σ link function: logit				
(Intercept)	-0.98	0.106	-9.273	< 0.05
trophic.guild-herbivores	0.969	0.117	8.251	< 0.05
trophic.guild-omnivores	0.461	0.135	3.407	< 0.05
trophic.guild-carnivores	0.819	0.143	5.709	< 0.05
spatial.extent	$-1.4 * 10^{-7}$	$3.9 * 10^{-7}$	-0.359	0.719
temporal.extent	$-6.1 * 10^{-4}$	$1.5 * 10^{-3}$	-0.401	0.688
richness	$-3.1 * 10^{-3}$	$8.6 * 10^{-4}$	-3.624	< 0.05

richness is positive, but only significant for the variation between low and highly positive skewness values (Table 4.4).

Table 4.4: statistical model coefficients for the skewness of the empirical datasets. The r^2 of the model is 0.15

Variable	category	Estimate	Std. Error	z score	p-value
(Intercept)	(0.5,1]	-0.038	0.268	-0.143	0.88
	[-1,-0.5)	-5.773	0.688	-8.39	< 0.05
trophic.guildherbivores	(0.5,1]	-0.882	0.276	-3.198	< 0.05
	[-1,-0.5)	3.138	0.478	6.571	< 0.05
trophic.guildomnivores	(0.5,1]	-1.492	0.342	-4.362	< 0.05
	[-1,-0.5)	2.322	0.788	2.946	< 0.05
trophic.guildcarnivores	(0.5,1]	-0.832	0.327	-2.548	< 0.05
	[-1,-0.5)	4.354	0.492	8.854	< 0.05
richness	(0.5,1]	0.012	0.003	4.427	< 0.05
	[-1,-0.5)	-0.314	0.224	-1.397	0.16

The three mammal trophic guilds show similar negative correlations between dominance and richness (panel (a) of Fig. 4.5, Pearson's ρ: -0.62 for herbivores, -0.66 for omnivores, -0.64 for carnivores). Regarding the relative rarity of the different guilds (panel (b) of Fig. 4.5), herbivores have the same proportion of species than of individuals in local communities (Wilcoxon signed-rank test, $W = 131422, p = 0.14$, Table A.4.1.3), whereas omnivores are comparatively more common (i.e. there are higher relative numbers of omnivore individuals than species, $W = 162226, p < 0.05$) and carnivores are rarer (there are more carnivore species than individuals, $W = 18772, p < 0.05$).
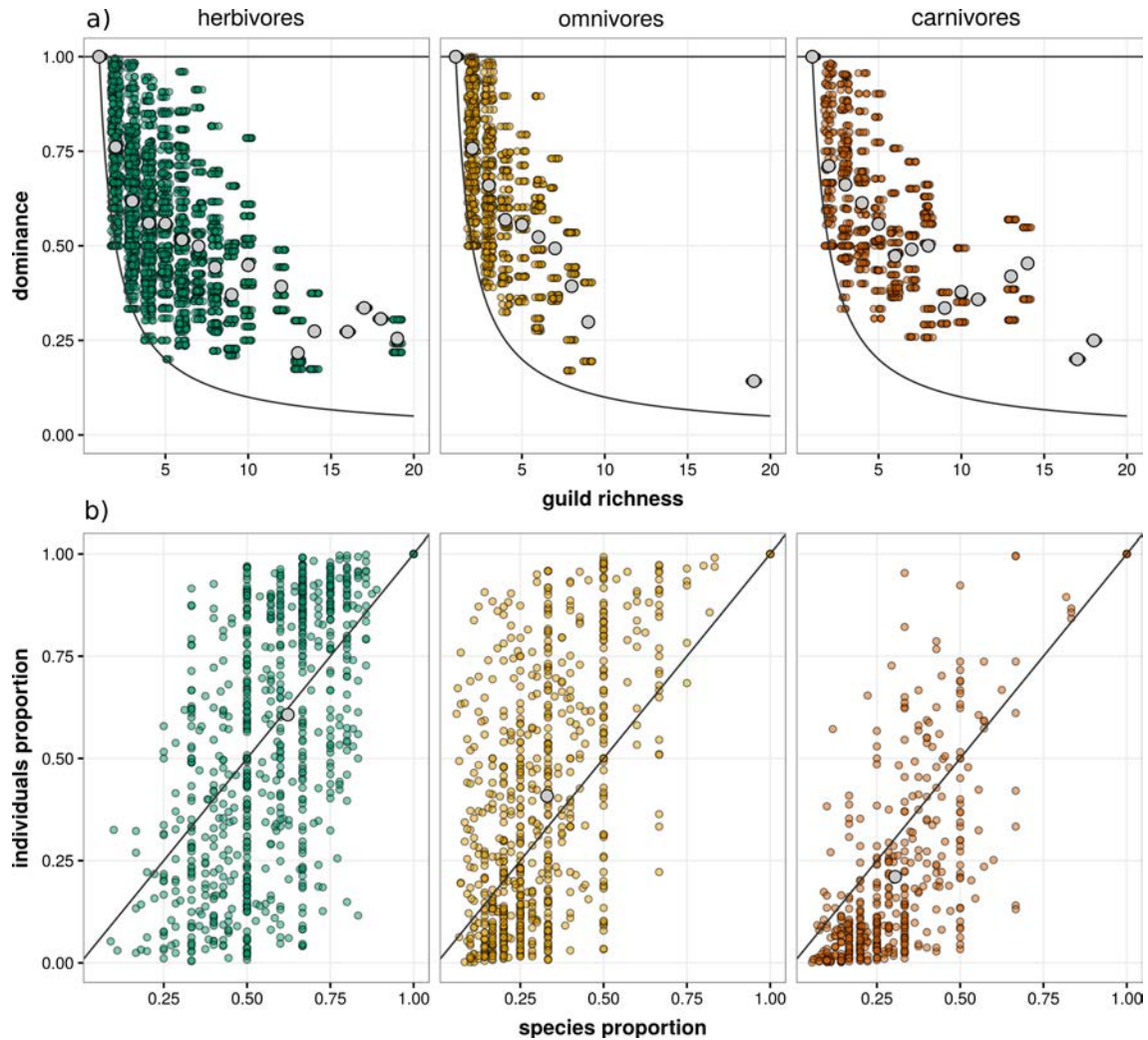
FIGURE 4.5: Patterns of dominance, and the proportion of species and individuals of the mammal guilds across sampling sites, where each point is a sampling site. Dominance (upper panel) is defined as the number of individuals of the most abundant species in the guild relative to all individuals from that guild. Minimum and maximum potential dominances are represented by solid curves. The maximum level of richness shown here, for visibility, is 20 species. The lower panel shows the proportion of individuals of a given guild against the proportion of species of the same guild, and the x=y line is shown for visibility. Grey-colored dots in both panels represent average values.

4.4 Discussion

In local communities, the division of species in trophic guilds is informative with regards to the distribution of interactions and biomass flows in the community (Lindeman, 1942; Kéfi et al., 2016), but everything else being equal, it is unclear wheter SAD metrics are influenced by the trophic position of a guild in the local community. Here I have shown that there are significant differences between the local SADs of terrestrial plant guilds (primary producers) and different guilds of terrestrial mammals, with plant SADs being less even and more skewed than mammal ones. Furthermore, the empirical relationship between SAD metrics and trophic guild is also mediated by species richness and the spatiotemporal

extent of the sample. A theoretical model combining network structure and niche apportionment schemes shows qualitatively similar trends in the variability of SAD shape across trophic guilds.

There are several potential ways of generating theoretical predictions about the variability of SAD metrics with trophic guild. Recent extensions to the theory of island biogeography (Holt, 2009; Gravel et al., 2011) make explicit the differences and feedbacks between species in discrete food chains, and could potentially be extended to predict the variability in species abundances across trophic levels. The model presented here, in turn, is meant to explore the role of local community structure in communities with a fixed number of species and no dynamic migration. In particular, the main question behind it is to explore whether variations in community structure (represented by species richness and network connectance) influence SAD shape of the increasing trophic guilds in model food webs.

I have shown that, given the assumptions of the model, evenness is highest (and skewness lowest) for herbivore species, and decreases for omnivore and carnivore guilds. Furthermore, community structure has significant impacts on both metrics: both richness and connectance have generally negative effects on guild evenness, and positive effects on the skewness of the SAD. With increasing richness or connectance, there is an associated increase in the number of trophic links for each species (its degree), so the general explanation for these patterns is that, under random fraction apportionment of resources, higher levels of resource overlap of the species within a given trophic guild drive higher heterogeneity in abundance distributions. Other niche apportionment schemes are likely to display different abundance patterns. For example, the *dominance preemption* scheme tends to produce highly heterogeneous distribution of resources and greater dominance levels than the random fraction apportionment. On the other hand, the *dominance decay* scheme will generate increasingly even abundance distributions with increasing richness or connectance (Tokeshi, 1990).

The empirical datasets analyzed here differ from the theoretical model in several fundamental aspects. Importantly, these datasets are likely to represent open communities, in which both core and transient species are observed, which has important implications for the associated SAD (Magurran and Henderson, 2003). Furthermore, they are not derived from entire communities sampled across trophic guilds, but are rather a compilation in which species are classified afterwards into broad guilds (see Methods). Therefore, analogies between the theoretical results and the empirical patterns should be approached with caution, due to these important confounding factors. However, the qualitatively similar variation of SAD metrics with trophic guild observed in theoretical (Fig. 4.3) and empirical data (Fig. 4.4) could also be due to empirical guilds displaying, on average, mechanisms of niche apportionment similar to the ones modelled. If we assume as a working hypothesis that some degree of niche preemption by dominant species takes place (Sugihara et al., 2003), the lower evenness and higher skewness observed in terrestrial plant communities relative to mammal ones may be explained by differences in the set of resources available to the different guilds. In particular, competitive exclusion may be higher in plant communities, leading to higher dominance of a few species, due to the comparatively small set of resources for which plants compete (light, water, and essential nutrients, Austin

and Smith 1990). Mammal guilds, in turn, may potentially have a wider variety of resources available. For example, mammal herbivores, as classified in this study and according to the *EltonTraits* database used to categorize trophic guilds (Wilman et al., 2014), can feed mainly on either seeds, fruits, nectar, pollen, and a large list of other plant parts. Therefore, a high degree of specialization within a guild may reduce the importance of competition and, subsequently, the relative differences in abundance between species (Sugihara et al., 2003). Such high specialization in trophic guilds is commonly observed in ecological networks (Dunne et al., 2002; Gravel et al., 2011).

Other complementary reasons for explaining the variation in SAD metrics between plants and mammals may exist. For example, differences in traits such as movement potential, which can make rare mobile mammal species harder to document, or unavoidable sampling inconsistencies between studies. It may also be the case that plant species are able to maintain lower densities for longer periods than mammal species, thus being more easily observed. Empirical estimates of minimum viable populations indicate that some plant populations may be viable with sizes of < 1000 individuals (Nantel et al., 1996), a number much lower than standard estimates for vertebrates, which range in a few thousands of individuals for their viability (Reed et al., 2003). Therefore, there may simply be more rare plant species than mammals'. Niche differentiation may also be invoked to explain the relative homogeneity in SAD metrics between mammal guilds. As it is the case with herbivores, both omnivore and carnivore guilds may utilize a wide set of resources that may, generally, prevent a high degree of competitive exclusion.

Mammal guilds also show a negative correlation between dominance and guild richness, suggesting that richer guilds may be generally more even via a decrease in relative dominance, a result in accordance with previous studies (Spencer, 2000; Dornelas et al., 2011). This results contrast with the theoretical model, in which evenness and richness are negatively correlated (Table 4.1). In empirical communities, the positive richness-evenness relationship may be due to the higher habitat complexity observed in richer communities (Hurlbert, 2004), a factor not included in the model that may lead to more diverse sets of resources and thus less importance of competitive exclusion. However, a negative relationship between richness and evenness has also been documented in different trophic guilds of grassland ecosystems (Bock et al., 2007). These contrasting results emphasize the need for controlled observations across different ecosystem types and productivity gradients. The only significant difference between mammal guilds found in this study is the relative rarity of carnivore species compared to those of other guilds, which also corroborates earlier results by Spencer (2000) on invertebrate communities. Overall, these broad-scale results will undoubtedly vary across habitat types, depending on the specific sets of resources available to each guild, and on the local environmental conditions, which may have contrasting effects on the different trophic guilds (Voigt et al., 2003).

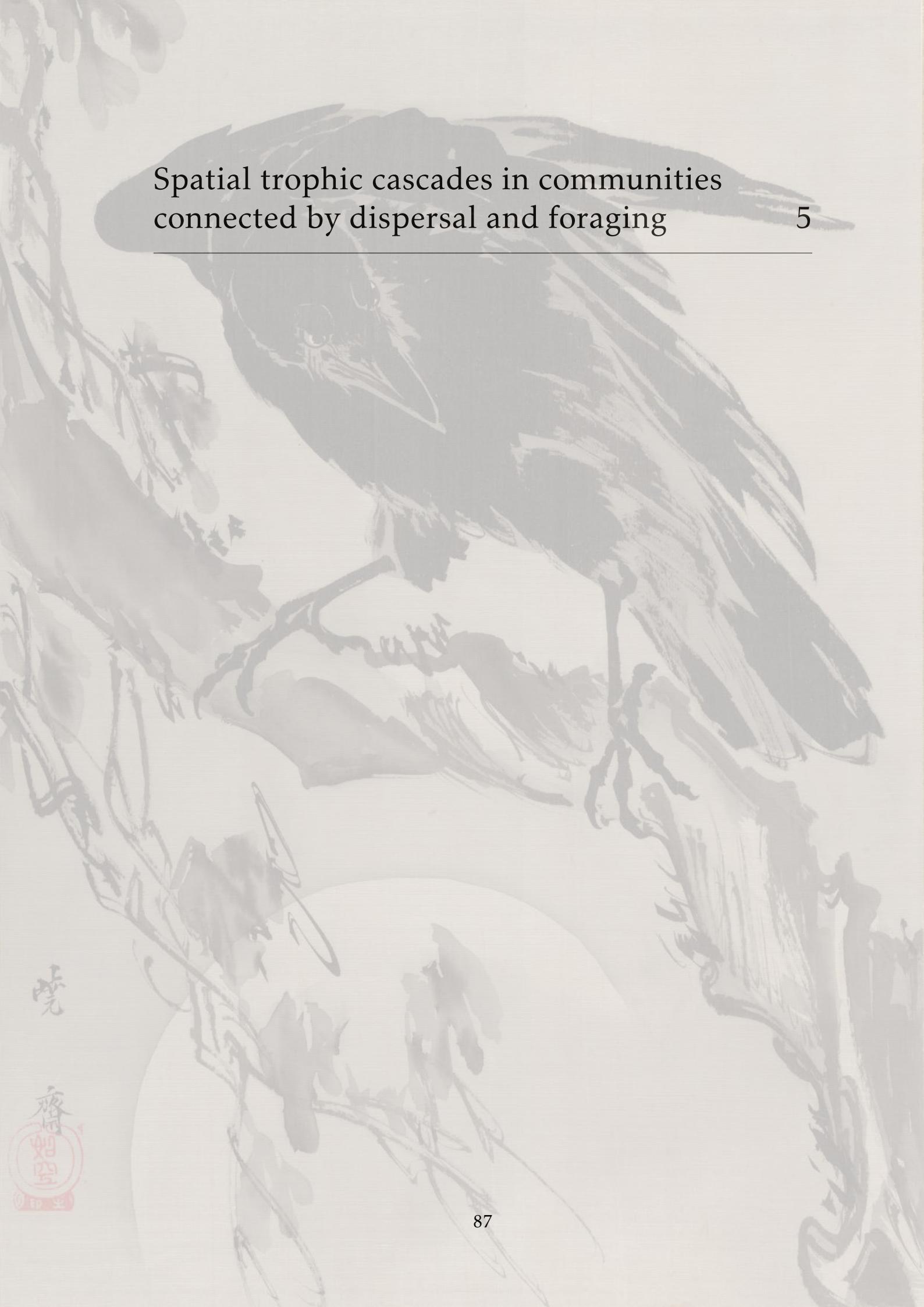All the results presented here assume that trophic interactions are the main driver of variation in species abundances across guilds. In the theoretical results, bottom-up energy flows from trophic interactions are the only ones considered, and the mammal communities were grouped considering only a general trophic guild classification of the species. This approximation is clearly a simplification

of the complex networks of interactions observed in nature, which may generate strong top-down or indirect feedbacks (Menge, 1995; Montoya et al., 2009). The persistence and abundance of all species in a community is further influenced by the whole set of interactions in which they engage, among other factors (Pocock et al., 2012; García-Callejas et al., 2018a). However, the distribution and frequency of most non-trophic interactions in empirical communities is not known, so no hypothesis can be formulated at this point regarding their influence on local SADs. In communities in which non-trophic interactions are known, functional guilds can be differentiated by accounting for the set of all interactions in which they engage rather than just trophic ones (Sander et al., 2015; Kéfi et al., 2016); this functional grouping may further reduce intraguild functional variability and thus increase across-guild differences, better reflecting differences in SAD shape across guilds. On the other hand, there is virtually an unlimited number of functional guilds in nature, and establishing a general, cohesive, and manageable set of functional guilds that can be applied to group every potential community seems unfeasible for the time being. Therefore, grouping by trophic guild represents a compromise between generality (as every community can be divided in such manner) and intraguild versus across-guild variability. In any case, the variability in SAD metrics across trophic guilds of a community, and its relationship with other factors, would be better explored with dedicated sampling campaigns of different trophic guilds in multi-trophic communities, in which properties such as trophic specialization can also be tracked. This could be carried out, for example, in pond mesocosms in which most species are confined to the pond habitat, or for terrestrial habitats, in small islands where complete censuses of different trophic guilds are feasible.

The existence of an intrinsic variability in SAD shape across functional guilds has important consequences for both fundamental and applied community ecology. In theoretical models, the contributions of intraguild and interguild interactions need to be integrated in a general mechanistic framework, in order for their relative importance to be estimated. This shift from intraguild, competitive interactions to multi-trophic, community scale thinking is a necessary step forward in theoretical community ecology (Chesson and Kuang, 2008; Godoy et al., 2018; Seibold et al., 2018). Empirical analyses of SADs would also benefit from incorporating information about the communities that harbor the guilds under study. In studies analyzing intraguild drivers of SAD shape, the community context of the study should be used to establish null expectations of interguild influence, for example, based on network structural patterns. If the guilds under study are not functionally homogeneous (e.g. taxonomic assemblages sensu Fauth et al. 1996) deriving mechanistic explanations about SAD shape is usually not possible, due to interspecific differences in resource use, trophic position, etc. In such descriptive studies, therefore, the community context is unnecessary. Meta-analyses of Species Abundance Distributions have shown great disparity regarding the most appropriate statistical models for fitting SADs (Ulrich and Gotelli, 2010; Baldridge et al., 2016). If the results presented here hold, accounting for this null expectation may help clarify which statistical models are best suited to fit each set of data.

4.5 Conclusions

Species Abundance Distributions have many axes of variability. Here I have showed that intrinsic differences exist between the SAD of terrestrial plant and mammal communities. Plant communities are significantly less even and more skewed than mammal ones, and there are no significant differences in either metric between the mammal trophic guilds considered. This result may arise from differences in niche availability for the different guilds, following the hypothesis that higher niche availability implies a higher evenness in species abundances. Although these results are derived from extensive datasets controlling for several factors, targeted studies are needed to further confirm this pattern and test it in a variety of systems. This prospective line of research would shed new light on both theoretical and applied analyses of Species Abundance Distributions, and would help in the integration of classic horizontal community ecology patterns in the context of communities encompassing multiple trophic levels and interaction types.

Spatial trophic cascades in communities connected by dispersal and foraging 5

Abstract

The effects of pairwise interactions have indirect consequences that reverberate throughout the whole ecosystem. In particular, interaction effects may propagate in a spatial dimension, to localities connected by organismal movement. Here we study the propagation of interaction net effects with a spatially explicit metacommunity model, when local sites are connected by dispersal, foraging, or by both modes of movement. We show that direct and net effects of pairwise interactions are more likely to be of different sign when foraging behaviours across localities are prevalent. Further, the effect of a species over another in the local community does not necessarily correspond to its effect at the metacommunity scale: this correspondence is again mediated by the type of movement mode across localities. The networks of net effects are in all cases fully connected, which means that every species in the model metacommunity has a non-zero influence in every other species, but network quantitative modularity differs with movement mode. Lastly, the magnitude of net effects between any two species strongly decays with the distance between them, specially with the number of indirect connections linking them. These theoretical results strengthen the importance of considering indirect effects across species at both the local and regional scale, point to the differences between modes of organismal movement across locations, and thus open novel avenues for the study of interaction effects in spatially explicit settings.

5.1 Introduction

Ecological communities are complex systems in which species interact with each other through a multitude of pathways. The effect of a species on the rest of the ecosystem is generally difficult to predict and quantify, and likely depends on factors such as the number and magnitude of interactions in which it engages (Zhao et al., 2016), or the structure of the overall network, that may enhance or decrease the propagation of the initial direct effects (Polis, 1994). Trophic cascades are striking examples of interaction effects propagating through food chains: changes in the occurrence, strength or outcome of a certain trophic interaction often have a significant top-down influence on the rest of the community (Schmitz et al., 2000).

Just as the spreading of disease (Balcan et al., 2009) or information (Barthélemy, 2011) in other types of complex networks, the propagation of interaction effects across ecological networks has an obvious spatial dimension: interaction cascades often link organisms that are spatially disconnected. Thus, we may define a *spatial cascade* as a set of indirect interactions that spread in a spatial dimension, potentially linking disconnected species. Spatial cascades thus defined are ubiquitous in nature, as in for example the connection of different regions by migratory animals (Springer et al., 2018) or, on a more local scale, the flow of dispersing individuals between separated locations (Leibold et al., 2004). Spatial cascades may occur between different locations of a single habitat type. For example, predator species may consume bird eggs from nests of different forest patches (Chalfoun et al., 2002), with potential feedbacks for the bird populations and associated resources.

The connections across different habitats by flows of nutrients or organisms have also been well documented (Polis et al., 1997). Focusing on the flow of organisms, just to note two prominent examples, Estes et al. (1998) documented how otter predation by killer whales in the open North Pacific triggered an increase in the biomass of sea urchins in the nearshore habitat of the Aleutian archipelago, ultimately driving a strong decline in kelp density. More recently, Knight et al. (2005) showed that the presence of predatory fish in ponds reduced the number of adult dragonflies in the surrounding area, which resulted in a significant increase in pollinator density and subsequent reproductive success of terrestrial plants, as compared to areas close to ponds without fish predation.

In a spatially explicit consideration of interaction cascades, unlike strictly defined trophic cascades (Ripple et al., 2016), both bottom-up and top-down effects may be involved, and these effects will likely differ in magnitude depending on the type of spatial flux or the trophic level of the connecting species (Allen and Wesner, 2016). For example, variations in the magnitude of plant dispersal between neighbouring locations will trigger bottom-up community-level responses on all sites (Christian, 2001). On the other hand, predators foraging on spatially disconnected patches may induce top-down indirect effects that may propagate across patches, either through consumptive effects that spread down the local trophic chains (Polis et al., 1997) or by non-consumptive effects on prey species (Orrock et al., 2008).

Overall, despite the growing number of studies documenting spatial propagation of interaction effects, the concept of spatial cascades has not yet been rigurously explored and generalized. For example, there are currently no theoretical hypothesis on the decay of interaction effects with spatial distance, or on whether different modes of movement generate similar or different patterns of effect propagation.

The net interaction effect between any two interacting species is, conceptually, the sum of their direct effects from pairwise interactions and indirect effects mediated by other species or entities (Abrams, 1987). The direct effects of a species over another can be formulated in several ways (Berlow et al., 2004), but generally involve the effects over some property of interest at the population level, such as short-term growth rate (Abrams, 1987). Indirect effects, in turn, involve all effects between two species that do not occur via direct interactions. Indirect effects may occur between species that interact directly or not, via the propagation of effects over the ecological network. These effects have been classified as being triggered by changes in the abundance of the intermediary species (*density-mediated indirect interactions*) or by these intermediary species modifying the context of a direct interaction (see e.g. Wootton 2002 for further definitions and examples). It has been repeatedly shown that indirect effects may be as strong, or even stronger, than direct effects, up to the point of switching interaction net effects from positive to negative or viceversa (e.g. Menge 1995). Therefore, analyzing how net effects are structured in complex communities, and their importance relative to direct effects, is an important step towards understanding and predicting the dynamics of ecological assemblages (Montoya et al., 2009).

The metacommunity concept (Leibold and Chase, 2018) provides a comprehensive theoretical framework for studying the propagation of interaction net

effects in a spatially explicit setting. In virtually all metacommunity studies we are aware of, it is assumed that species connect the local communities via dispersal, i.e. the permanent establishment of individuals on a different territory from their birthplace. Dispersal, however, is not the only process by which species can link spatially disconnected patches. Foraging, the active search for food of a mobile individual, may link the trophic chain of its reproductive area with other, potentially disconnected communities in which the individual acquires varying fractions of its diet (McCann et al., 2005). If foraging species are based on a central site, which may well be their reproductive area, their foraging effort and associated effects on local communities generally decay with distance, in what is termed *Central-place foraging*, (Orians, 1979). Just as with dispersal, the spatiotemporal dynamics of foraging are extremely varied, with variation in home ranges spanning several orders of magnitude (as an indicator, Swihart et al. 1988 showed that home range in 23 species of mammals varied from 0.05 to 2285 ha). Of course, both foraging and dispersal modes of movement occur in nature and are not independent from each other, but as a first approximation, we may expect spatial cascades triggered by each movement type to display different properties and effects on the connected local communities (Fig. 5.1). For example, in two simple food chains connected by a dispersing species, the net flow of individuals from one community to the other will benefit the predators of the dispersing species, and in turn, adversely affect its prey. On the other hand, if the same species connects the two food webs by foraging sporadically on the second location, it will trigger a negative effect up the trophic chain of that location, and will benefit species on which the preyed species feeds.

Here we study how net effects are propagated in space when local food webs are connected by dispersal, foraging, or a combination of both movement types, using model metacommunities. In particular, we ask the following questions: (1) What is the distribution of signs and magnitudes of net effects in communities connected by dispersal, foraging, or a mixture of both? (2) Are networks of net effects similar in structure to networks of direct effects? (3) Does the magnitude of the net effects between any two species decay with increasing distance between them?
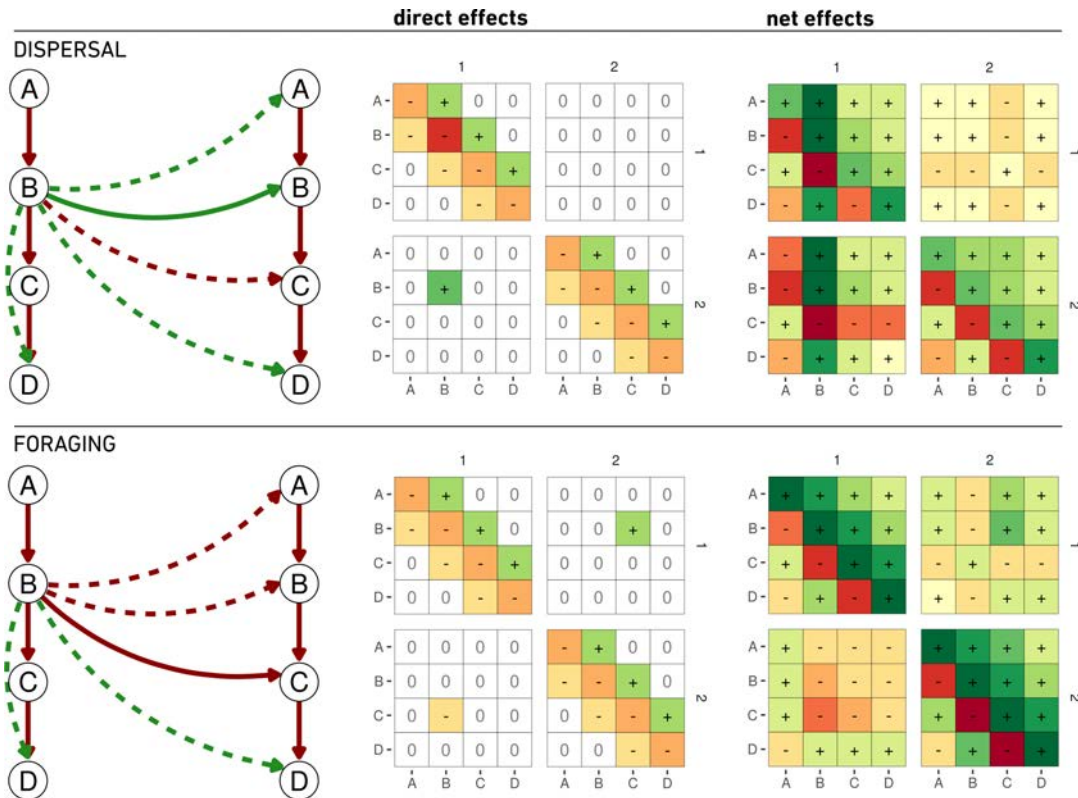
FIGURE 5.1: Interaction matrices and net effect matrices for two simple configurations. In both cases, a linear food chain is represented at two locations (*1* and *2*). In the dispersal configuration, species B disperses from the first location to the second. In the second configuration, species *B* preys on species *C* on both locations. Green links represent positive effects, red negative. Solid arrows represent direct effects, dashed arrows expected indirect effects. For clarity, in the food chains we display only the indirect effects arising directly from species *B* at location *1*. Darker shades in the matrices indicate stronger effects. The matrices can be read as with the following example: in the foraging configuration, the direct effect of *B* in location *1* over *C* in location *2* is given by locating the column that indicates species *B* at location *1* (the second column of the matrix), and the row indicating species *C* at location *2* (seventh row).

5.2 Methods

We developed a spatially explicit metacommunity model in which local trophic communities are connected through 1) dispersal, 2) foraging, or 3) both. The dynamics of the system are given by a general Lotka-Volterra implementation, following Gravel et al. (2016*b*), and for each configuration we ran numerical simulations and recorded both the direct effect and the net effect between each pair of species in the metacommunity, as well as a set of network metrics for characterizing potential differences in metacommunity structure.

Quantification of direct and net effects

In theoretical analyses of ecological networks, the Jacobian matrix of the system (also called *community matrix*) is widely used to describe the direct effects between each pair of species at equilibrium. In its most common implementation, it

represents the effect in one species' growth rate respect to small changes in another species' abundance (Berlow et al., 2004; Novak et al., 2016). Consider a general population dynamics model of S species present in n local sites, in which the population density of species i at site x over time is given by

$$\frac{dN_{ix}}{dt} = N_{ix}f_{ix}(N_1.,...,N_S.)$$ (5.1)

where N_{ix} is the density of species i in site x, and $f_{ix}(N_1.,...,N_S.)$ its growth rate, potentially influenced by any other species present in any of the n sites (represented by the $\cdot$ notation). In this general case, the elements of the metacommunity Jacobian matrix C are

$$c_{ix,jy} = \frac{\delta(\frac{dN_{ix}^*}{dt})}{\delta N_{jy}^*} = \frac{\delta[N_{ix}^* f_{ix}(N_1^*.,...,N_S^*.)]}{\delta N_{jy}^*}$$ (5.2)

where N_{ix}^* represents the steady state density of species i at site x. The net effect of species j at y over species i at x, in turn, is the sum of its direct effects and all indirect effects between the two species evaluated at steady state (Bender et al., 1984; Montoya et al., 2009; Novak et al., 2016). These can be calculated as the negative of the elements of the inverse Jacobian, i.e. $-(c^{-1})_{ix,jy}$. Specifically, the coefficients $-(c^{-1})_{ix,jy}$ represent the net effect of an increase in species j's population growth rate on the density of species i, when all species respond to direct effects (Novak et al., 2016).

The model

The dynamics of the community are modelled with a general Lotka-Volterra implementation, following Gravel et al. (2016b). Considering a set of S species present at n locations, the dynamics of species i at location x is given by:

$$\frac{dN_{ix}}{dt} = N_{ix}(m_{ix} + \sum_{y\in n}\sum_{j\in S} b_{ix,jy}N_{jy}) + \Delta N_{ix}$$ (5.3)

where m_{ix} is the intrinsic growth rate of species i at location x, N_{ix} its abundance, ΔN_{ix} is the net migration balance, and $b_{ix,jy}$ is the per capita effect of species j at location y on species i at location x. This parameter encapsulates the effect of foraging to/from other locations, and it represents a basic situation in which species i forages from its reproductive area x to other locations. Specifically, we assume that a foraging species allocates a fraction f of its foraging efforts to communities outside its reproductive location, which implies that the effort

allocated to feeding in its local community is $1 - f$. We incorporate this in our model as follows:

$$
b_{ix,jy} = \begin{cases} (1-f)\alpha_{ix,jy} & \text{if } x = y \\ \dfrac{f}{|n_{ix}|}\alpha_{ix,jy} & \text{if } x \neq y, \alpha_{ix,jy} > 0 \\ \dfrac{f}{|n_{jy}|}\alpha_{ix,jy} & \text{otherwise} \end{cases} \tag{5.4}
$$

The first situation corresponds to the effect of predation from the same location, in which case the interspecific interaction coefficient $\alpha_{ix,jy}$ is weighted by the relative effort dedicated to foraging within its home location $(1 - f)$. The second situation represents foraging of species i at location x on species j at location y. The net foraging effort f is equally divided among all locations reachable by species i from location x (the set given by n_{ix}, which has a cardinality of $|n_{ix}|$). The last situation is the opposite, where species i at location x is preyed upon by species j at location y. In this case, f is divided among all locations reachable by species j from location y. Note that this situation represents an equal division of foraging effort among all reachable locations.

Dispersal among different locations, in turn, is represented simply by the net variation in species densities between reachable locations, modelled by passive diffusion with dispersal coefficient d (Gravel et al., 2016b):

$$
\Delta N_{ix} = \sum_{y \in n_{ix}} \frac{d_{ixy}}{|n_{ix}|}(N_{ix} - N_{iy}) \tag{5.5}
$$

Thus, as it is the case with foraging, dispersal effort d is divided equally among all patches reachable by species i on location x.

Parameterization and simulations

We considered predator-prey interactions, but the approach could easily be generalized to other types of interactions. The structure of local communities, i.e. who interacts with whom, is determined according to the niche model (Williams and Martinez, 2000), ensuring that there were no disconnected species. We further assumed that the niche axis obtained from the niche model is linearly correlated with the foraging and dispersal distance of the different species, such that the species with lowest niche values could only forage or disperse to adjacent communities. Interaction coefficients α at the regional scale are drawn from a normal distribution $N(0.25, 0.1)$, with the sign structure given by the niche assembly model. We introduced a small amount of spatial heterogeneity by drawing local coefficients from a normal deviate with mean centered on the corresponding regional coefficients and standard deviation of 0.1.

Local communities were placed along a single dimension space, which ends were connected together in order to (1) maximize potential path lengths between

non-connected communities, and (2) prevent edge effects of communities at the end of the linear chain. We fixed the maximum dispersal and foraging distances to two cells away from the species' home location in order to avoid excessive parameterization and for better comparing the net effects of the different movement types.

With this setting, we simulated the dynamics of 15 species at 10 local communities. The number of species and size of the landscape correspond to a meta-adjacency matrix of $15 * 10 = 150$ rows. This size was chosen in order for the numerical calculation of the Jacobian matrices to be computationally feasible. Although a relatively small species richness and number of patches, it is sufficient to explore spatial distances and patch lengths of over 5 units.

We generated three sets of simulations: only dispersal, in which we set the dispersal coefficient $d = 0.5$, and the foraging coefficient $f = 0$ for every species; only foraging, with $d = 0$ and $f = 0.5$; and dispersal and foraging, with $d = 0.5$ and $f = 0.5$.

We run 100 random topologies from each configuration, and for each replicate we obtained numerically the direct and net interaction coefficients between each pair of populations in the metacommunity, which could then be (1) qualitatively compared and (2) analyzed with regards to the distance between the interacting populations. We also computed basic quantitative descriptors of the direct and net effects networks at equilibrium: the *connectance* of the metacommunity networks; their *average path length*, i.e. the average of the shortest path lengths between any pair of populations in the metacommunity; and their *modularity*, which measures the tendency for nodes to be grouped into distinct modules (Newman, 2006). Here, we calculate a weighted version of modularity that considers both positive and negative link weights, as implemented in the R *igraph* package (Csardi and Nepusz, 2006).

5.3   Results

What is the distribution of signs and magnitudes of net effects in communities connected by dispersal, foraging, or a mixture of both?

Net effects (i.e. elements $-(c^{-1})_{ix,jy}$ described above) are mainly of equal sign as direct effects (i.e. elements $c_{ix,jy}$ of the Jacobian matrix) when local communities are connected by dispersal (Table 5.1), whereas in foraging and mixed modes of movement, sign switches occur in around 50% of pairwise interactions. In all simulations, however, the ratio of positive to negative net effects is maintained at values close to 1, meaning a similar number of positive and negative net effects for all configurations.

The three modes of movement displayed distinctly different net effects signatures on interactions occurring both within the same location (intra-patch) and across different locations (inter-patch) (Fig. 5.2). Intraspecific effects are generally positive across locations in the dispersal configuration, and also positive in the local food webs (upper panel of Fig. 5.2). This trend is blurred for foraging and

Table 5.1: Summary metrics of the simulations performed. For each simulation, we group the results by location, i.e. whether the interaction occurs between species of the same (intra-) or different (inter-) patch. We show the ratio of positive to negative net effects, and the relative frequency of pairwise interactions that switch sign from direct to net effect.

movement mode	location	+/- ratio	sign switches	
			+ to -	- to +
dispersal	intra-patch	0.95	0.07	0.33
	inter-patch	1.03	0.002	0
foraging	intra-patch	1.02	0.51	0.47
	inter-patch	0.97	0.42	0.41
dispersal and foraging	intra-patch	1.02	0.52	0.57
	inter-patch	1.02	0.48	0.49

mixed movement modes, where intraspecific effects are more variable and have a higher frequency of negative magnitudes (Fig. 5.2 middle and lower panels). Net effects are also generally of the same sign in local patches and across patches when communities are connected by dispersal (orange points on the upper panel of Fig. 5.2). Again, this trend is diluted when foraging is accounted for, in which case intra-patch and inter-patch net effects display any combination of positive and negative signs, with no clear trend. Although here we analyze the results for $d = 0.5$ and $f = 0.5$, the distinctiveness of the dispersal and foraging patterns is maintained across a range of d and f values (Appendix 5.1).
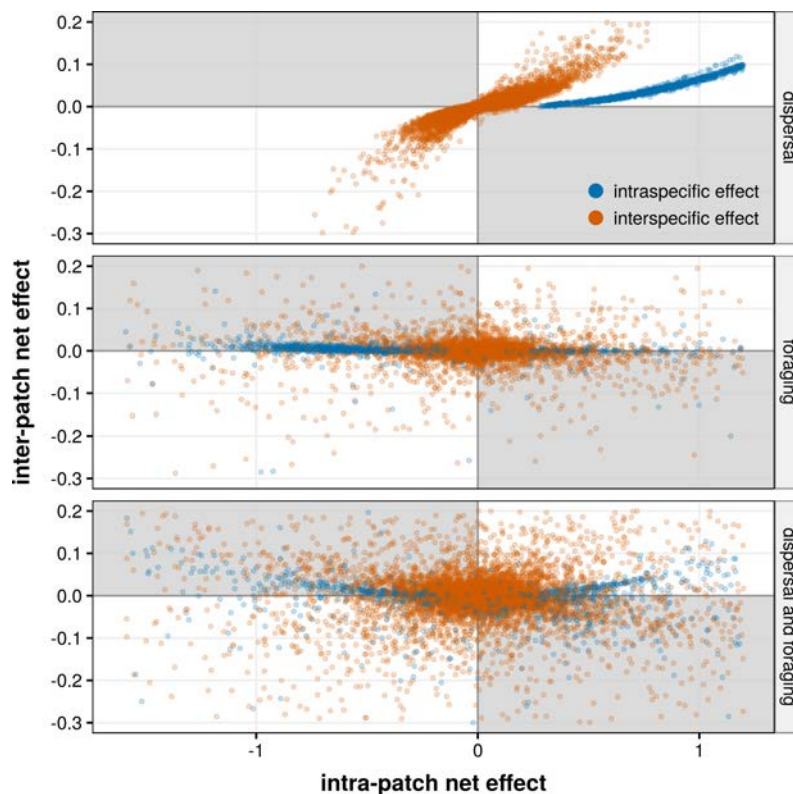
Figure 5.2: Distribution of intra and inter-patch net effects in the three configurations. Shaded quadrants are those where a sign switch occur between intra and inter-patch effects.

Are networks of net effects similar in structure to networks of direct effects?

There exist non-zero net effects between virtually every species in the model metacommunities, as expressed by net effect networks having connectances and path lengths of 1 in all cases (Fig. 5.3). In contrast, direct effect networks are obviously not fully connected, displaying intra-patch connectances at steady state of 0.38 on average and inter-patch connectances between 0.01 (dispersal only) and 0.1 (dispersal and foraging). Weighted modularity is also much higher in the direct effects networks than in the net effects ones, as expected. However, the modularity of the net effects networks also shows a decreasing trend from dispersal only networks to dispersal and foraging ones (Fig. 5.3).
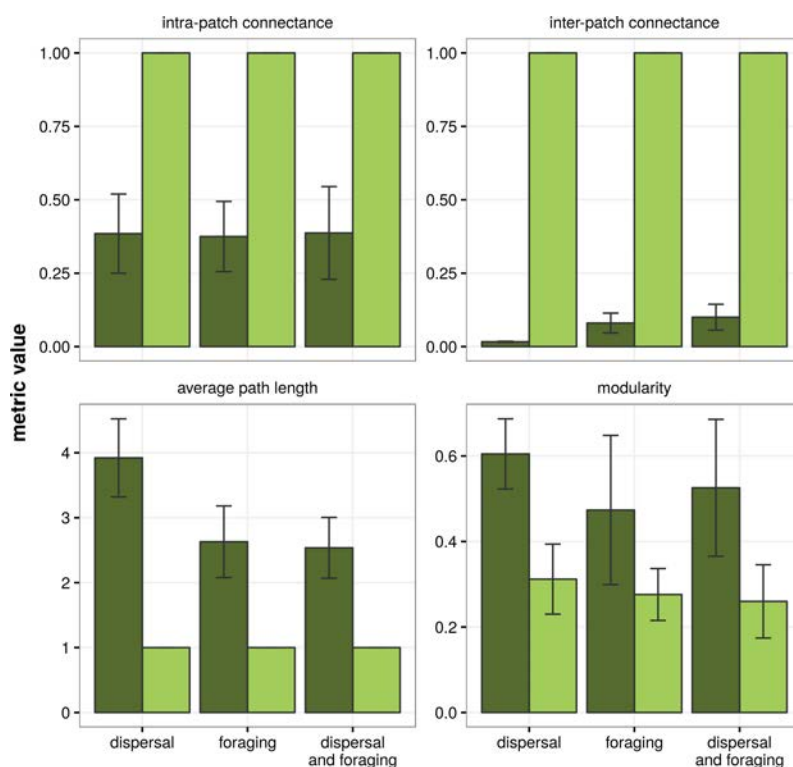
Figure 5.3: Network metrics of the metacommunities at equilibrium. Dark shades represent networks of direct effects, light shades networks of net effects.

Does the magnitude of the net effects between any two species decay with increasing distance between them?

The magnitude of spatial cascades is influenced by the length of its associated food chain. Net effects between any pair of species decrease in magnitude with the spatial distance between the two species (i.e. the distance between their home locations, assuming that connected locations are at distance 1 from each other). This decrease is even sharper when the distance metric considered is the path length between the two species, i.e. the number of connections separating them (Fig. 5.4). This result is observed in the three movement modes, although the

decay rate is generally highest for foraging configurations. The trend is also robust to variations on dispersal and foraging rates (Appendix 5.1).
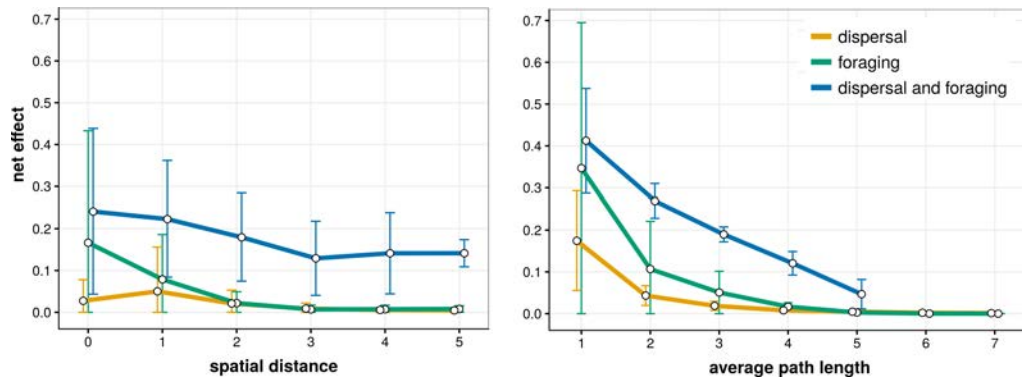
FIGURE 5.4: Net effect between species pairs as a function of *a)* spatial distance between patches, *b)* average path length between species. Values are averaged over all replicates, and error bars represent averages +/- one standard deviation.

5.4 Discussion

The importance of indirect effects, including trophic cascades, in driving ecosystem dynamics and structure is well established in theory (Abrams, 1992; Wootton, 2002; Gravel et al., 2010; Mayfield and Stouffer, 2017) and on the field (Menge, 1995; Peacor and Werner, 1997; Moya-Laraño and Wise, 2007; Barbosa et al., 2017; Trussell et al., 2017). The propagation of these effects across space has however not been studied systematically, despite many scattered observations of spatially explicit trophic cascades (Polis et al., 1997; Estes et al., 1998; Knight et al., 2005; Casini et al., 2012; Springer et al., 2018). Here we lay down basic tenets on how interaction effects are propagated in space depending on whether species connect different local communities via dispersal, foraging, or both modes of movement. We show that model metacommunities with populations connected by dispersal and foraging differ on (1) the proportion of pairwise interactions that switch sign between their direct and net effects, and (2) the sign and magnitudes of net effects on the local patch and across patches. Furthermore, the networks of net effects are markedly different from the direct effect ones, in all cases. Last, we observed that, in most cases, the magnitude of net effects between any two populations decays significantly with the distance between the two populations. In particular, the strongest decay occurs when distance is measured as the number of spatial connections necesary for linking the two populations.

Indirect effects may generate unexpected net interaction outcomes between pairs of species. For example, Montoya et al. (2009) analyzed a set of well-resolved empirical food webs and showed that the influence of indirect effects induced a switch in interaction signs from direct to net effect for approximately 40% of species pairs. Using a similar approach, we show that net effects between populations of spatially disconnected communities may also be primarily driven by indirect feedbacks, as for example, cases in which a species foraging on a

secondary location indirectly benefits its prey on this second location by altering the dynamics of the whole food web. This theoretical possibility has, to our knowledge, not been tested in empirical systems.

The "signatures" of net effects produced by dispersal, foraging, or mixed modes of movement across localities are clearly different from each other (Amarasekare, 2008) even though we imposed equal maximum dispersal and foraging distances, and after accounting for different values of dispersal and foraging rates (Appendix 5.1). In the dispersal scenario, the almost complete concordance between the sign of intra- and inter-patch net effects points to a relatively homogeneous role of species at local and regional scales. Therefore, in natural systems with the same species pool connected mainly by dispersal, a local evaluation of the influence of the dispersing species may offer insights for the whole metacommunity. In the foraging or mixed modes, however, interspecific net effects derived from the populations of the same and different locations often switch signs, without showing any clear trend (middle and lower panels of Fig. 5.2). Therefore, within the assumptions of our model, when foraging is a prevalent mode of movement across locations, interspecific effects between any two species cannot be extrapolated from the local to the regional scale. In other words, a consumer that decreases a prey locally may have a positive effect on the same prey at the regional scale. Note, however, that our baseline scenario represents communities within an homogeneous habitat, the same species pool in all locations, with no density-dependent movement modes, no active selection or other types of heterogeneity. Furthermore, we deliberately chose dispersal and foraging modes of movement with identical maximum distances and temporal dynamics, in order to highlight their intrinsic differences. In reality, of course, both dispersal and foraging have extremely variable spatiotemporal scales. Foraging, in general, happens much faster than local demographic dynamics, which has led to characterize its effects as *spatial coupling* of local communities (Massol et al., 2011). This spatial coupling is thought to dampen population oscillations at lower trophic levels (McCann et al., 2005). The effects of dispersal, on the other hand, occur on temporal scales comparable to those of local dynamics, favouring different types of coexistence relationships, such as source-sink dynamics. The relative scales of foraging and dispersal are very heterogeneous, so that the spatial signal of interaction cascades will likely be correlated, in general, with these movement-related traits. In our model, we restricted the maximum dispersal and foraging rates to two cells away from the local community, and different values will presumably alter the net effect decay with spatial distance (Fig. 5.3 left panel). Interestingly, the decay of net effects with path length (Fig. 5.3, right panel) did not vary strongly with increases in maximum movement rates in our model (d and f, see Appendix 5.1). This result suggests that indirect effects may dampen the propagation of strong interactions across space, at least in environments with similar habitats and species pools.

Networks of net effects are fully connected (Fig. 5.3), meaning that every species has a non-zero influence in every other species of the metacommunity, through direct and/or indirect pathways. The number of connections between local communities increases from dispersal to foraging modes, and is maximal when both modes are combined. This is reflected in the weighted modularity of the net effects networks, which tends to decrease along that axis. In the simple

metacommunities modelled here, these structural patterns of the net effect networks are mostly confirmatory, but such analyses, when feasible, should provide novel insights into the structure and dynamics of more complex communities and metacommunities.

Dispersal generally represents unidirectional organismal movement across localities, with no associated direct movement of material. Foraging, on the other hand, involves a processing of organic material from the foraged location to the home location (Gounand et al., 2018). This two-way coupling has consequences for the role of the different locations as demographic sources or sinks (Gravel et al., 2010). In general, although here we have focused on movements of organisms across localities, the physical transfer of material often plays a key role in the structure and dynamics of the local communities (Polis et al., 1997). For example, the nutrients accumulated by Pacific salmon in open waters are transported to freshwaters during the spawning season, indirectly affecting terrestrial plants and animal populations (Naiman et al., 2002; Levi et al., 2012). The integration of these *ecological subsidies* with organismal movement is well developed theoretically in the framework of metaecosystem theory (Loreau et al., 2003; Gounand et al., 2018). We have provided a first approach to the explicit modelling of foraging behaviours in metacommunities, but its coupling with material transfers will expand and refine the results presented here. In a related question, most empirical studies on ecological subsidies are focused on transfers between different habitats, which usually involve specialized interactions (e.g. the consumption of Pacific salmon by grizzly bears) or species with life stages in different habitats, such as arthropods with aquatic larval stages that, in their adult form, switch to a predator role in terrestrial habitats. We, in turn, modelled communities with a small amount of spatial heterogeneity but the same pool of species and interactions on each patch. It is likely that interactions connecting different habitats are more specialized and have greater indirect effects than the general foraging interactions modelled here (in what has been called *keystone interactions*, Helfield and Naiman 2006). This specificity is likely to alter both the structure of the overall meta-network (Fig. 5.3) and the distance decay curves observed in our model system (Fig. 5.4). For example, Knight et al. (2005) showed how predatory fish could have strong net effects on terrestrial plants through a series of specialized interactions, even though the number of links separating these species is four (fish-dragonfly larvae-dragonfly adults-insect pollinators-plants).

Spatial patterns of net effects can also vary from our baseline expectations depending on the distances covered by the foraging or dispersing species. Intercontinental migrations are an extreme example of this, where strong coupled effects occur between species separated by thousands of kilometers (Alerstam and Bäckman, 2018). Further, such migratory movements connect localities at different moments in time, rather than continuously. The effect of such temporal decoupling may provoke strong oscillatory dynamics between systems (Springer et al., 2018), although in general, the stability dynamics associated with migrations have received little attention to date. Overall, the interplay between the rates and distances of dispersal and foraging, and their relationship to the spatial decay of net effects, clearly needs more attention in theoretical models and empirical studies. For example, experimental mesocosms allowing spatial movement

of certain species among them may be used to test the differential influence of foraging and dispersal on local dynamics.

5.5 Conclusions

We have provided a theoretical basis to the study of spatial propagation of indirect effects across ecosystems. We have shown that the net effect patterns generated by dispersal and foraging movements are clearly different. Furthermore, the structure of the metacommunity networks is markedly different depending on whether one considers direct interactions or net effects between species. The decay of net effect magnitude with distance, in our model, is the only result common to all simulations performed. These results may shed light on the spread of interaction effects in patches of the same habitat type, such as forest patches inserted in agricultural or urban areas. Furthermore, they represent a baseline case for developing more complex scenarios, such as the effects of interaction spread (1) across different habitat types and species pools, or (2) when material fluxes are accounted for.

Community responses to resource and non-resource environmental gradients 6

Abstract

Environmental variations are a driving force behind virtually all ecological patterns. Different types of environmental gradients are bound to trigger differential responses at the species and community level, but this variability among environmental factors has been largely overlooked in current community ecology paradigms. We argue that the distinction between resource and non-resource factors, originally proposed by Evelyn G. Hutchinson, provides a convenient way to classify environmental factors, as these two types have different effects on ecological interactions and emergent community properties. Using a community model with environmental variability on a resource and a non-resource factor, we show that the intensity of competitive interactions is driven jointly by variations in both gradients, whereas facilitation intensity is driven solely by the non-resource factor. Likewise, species richness and persistence times of species are mainly driven by variations in the non-resource factor. These results, derived for simple model communities, suggest the possibility that these two broad types of environmental gradients trigger different bottom-up and top-down feedbacks in more complex communities.

6.1   Introduction

Understanding how environmental factors influence ecological processes is one of the main goals of ecology, and is becoming increasingly relevant in the context of the ongoing global change (Vitousek, 1994). Environmental factors influence directly or indirectly virtually every biological process on Earth, and can be extremely varied in their physical characteristics, magnitude, spatial and temporal scale. Furthermore, individuals may interact and respond to their physical environment in very different ways: sessile primary producers acquire inorganic nutrients from their surrounding environment and can often modify their local microclimate, whereas animals are able to move or alter their behaviour in response to environmental variations. Despite the enormous variability in environmental variables and species responses, different environmental factors are commonly lumped together when studying ecological processes across observed gradients, in what are termed "(environmental) stress gradients" (e.g. Hart and Marshall 2013).

As a consequence of this common simplification of environmental factors, there is no overarching theory predicting how different facets of the environment will influence ecological processes at different levels of organization. Developing, or as we will suggest here, recovering a simple but comprehensive "taxonomy" of environmental factors is a key step towards such a theory. To our knowledge, only a handful of studies have attempted to derive a systematic characterization of environmental factors. For example, Menge and Sutherland (1987) made the distinction between physical and physiological stress types, that differ on whether low values of the factor at hand influence survival. Although their classification is readily applicable to any species and gradient, it is not informative about which factors may drive variations in pairwise interactions or resource consumption, which are key processes for maintaining species coexistence.

In the context of niche theory, Evelyn G. Hutchinson (1978) proposed the distinction between scenopoetic and bionomic variables that shape the n-dimensional environmental niche of a given species. Scenopoetic variables are, literally, "scene-setting" factors, abiotic conditions that cannot be consumed, whereas bionomic variables are those consumed by the species or guild in question, thus altering their local dynamics. This distinction has been acknowledged, with a different terminology, in studies of vegetation composition across gradients (Austin and Smith, 1990). In addition, the stress gradient hypothesis, in its general form, posits that variations in stress levels will drive variations in the intensity of competitive and facilitative interactions among primary producers, with positive interactions becoming more prevalent under harsh conditions (Bertness and Callaway, 1994). A few studies have explored how this hypothesis might be improved by distinguishing resource (i.e. bionomic) and non-resource (scenopoetic) environmental factors. For example, a recent study suggested varying outcomes of pairwise interactions under gradients of different types of factors (Maestre et al., 2009), whereas a compilation of empirical data showed similar shifts towards facilitative interactions across gradients of different stress types (He et al., 2013). Despite these recent developments, most empirical tests of the stress gradient hypothesis do not explicitly consider the implications of studying resource, non-resource, or combined gradients. Furthermore, this diversity of factors has thus far been left out of other influential frameworks in community ecology, such as Tilman's resource ratio theory (Tilman, 1980; Miller et al., 2005), environmental stress models (Menge and Sutherland, 1987), or Chesson's coexistence theory (Chesson, 2000).

We propose to reintegrate the fundamental distinction between environmental factors coined by Hutchinson (1978) into current ecological paradigms. Hutchinson's categorisation provides a simple dichotomy for environmental factor types that is relevant for evaluating physiological responses, and most importantly, the outcome of direct pairwise interactions and other community-level responses to environmental gradients. Maintaining the terminology that has recently been developed under the umbrella of the stress gradient theory, we propose to keep the name of resource and non-resource environmental factors for bionomic and scenopoetic variables respectively (Fig. 6.1).

While at the individual level most species will display varying physiological response curves for specific factors regardless of their resource or non-resource quality, the distinction between these categories becomes important when looking at the differences of these response curves between species. As such, we may expect responses to resource factors to be nested for groups of species, while responses to non-resource factors will likely tend to have different optima for different species of a guild (Austin and Smith, 1990).

Looking at community-level responses, we hypothesize that variation in resource factors will directly drive exploitative competition within species of the same trophic guild, whereas variation in non-resource factors will, instead, drive changes in the intensity and importance of facilitation, and only indirectly will affect competition. These pairwise effects will, in turn, drive different outcomes for species persistence or diversity, among other properties, across different types of gradients.

Here we test these hypotheses using a community model in which we incorporate gradients of resource and non-resource environmental factors. In particular, we ask: (1) does the intensity of competitive and facilitative interactions vary across a combined resource and non-resource environmental gradient? (2) how are species diversity and persistence affected by environmental variation? (3) does the presence of benefactor species increase species diversity and persistence in our model communities? In the following sections, we briefly expand on the two types of environmental factors proposed, and then we discuss our modelling experiment.

6.1.1   Non-resource environmental factors

Non-resource factors are the scenopoetic variables of Hutchinson (1978), not consumed by individuals, and thus not subjected to depletion. These factors have a direct physiological impact on all individuals, and many of them are expected to have broad spatial structures (Soberón, 2007). Response curves may show different optima for different species, and are unimodal (Austin and Smith, 1990). There are two main ways in which species can alter these factors: first, sessile species may passively generate microhabitats with different conditions from those of the surrounding area. Second, some mobile species are considered ecosystem engineers, species that actively modify their surrounding physical environment thus generating different conditions.

By varying their surrounding environment, sessile species and ecosystem engineers generate environmental conditions that allow the establishment of other individuals that would not be able to thrive otherwise. Thus, facilitative interactions are commonly found to increase in intensity with increasing stress from non-resource factors such as temperature or wind exposure (e.g. Fajardo and McIntire 2011). By definition, as these factors are not subject to consumption, non-resource gradients will not directly drive variations in competition intensity (although by excluding less adapted individuals, overall competition intensity is often reduced in sites with high non-resource stress).

6.1.2   Resource environmental factors

This category includes all factors that are consumed by the species or guild under study. When referring to terrestrial plants, the set of resources is limited to light and space, water, carbon dioxide, oxygen, and essential nutrients (Austin and Smith, 1990). Each of these resources, in turn, has different spatiotemporal dynamics. Conceptually, feeding sources of consumer species may be considered as resource factors, but these resources are highly dynamic and consumers are often able to switch between different preys, whereas abiotic resources are generally not interchangeable.

Gradients in resource factors will drive variations in exploitative competition when different individuals utilise the same resource. On the other hand, these factors are generally not subject to facilitation, and therefore, the intensity of pairwise facilitation should in general not vary when the only source of environmental variation is a resource factor. As discussed in Maestre et al. (2009), the

case of water availability is more complex than this baseline expectation, as water availability is highly correlated with temperature levels, and may be subject to facilitation under some circumstances (see Discussion).
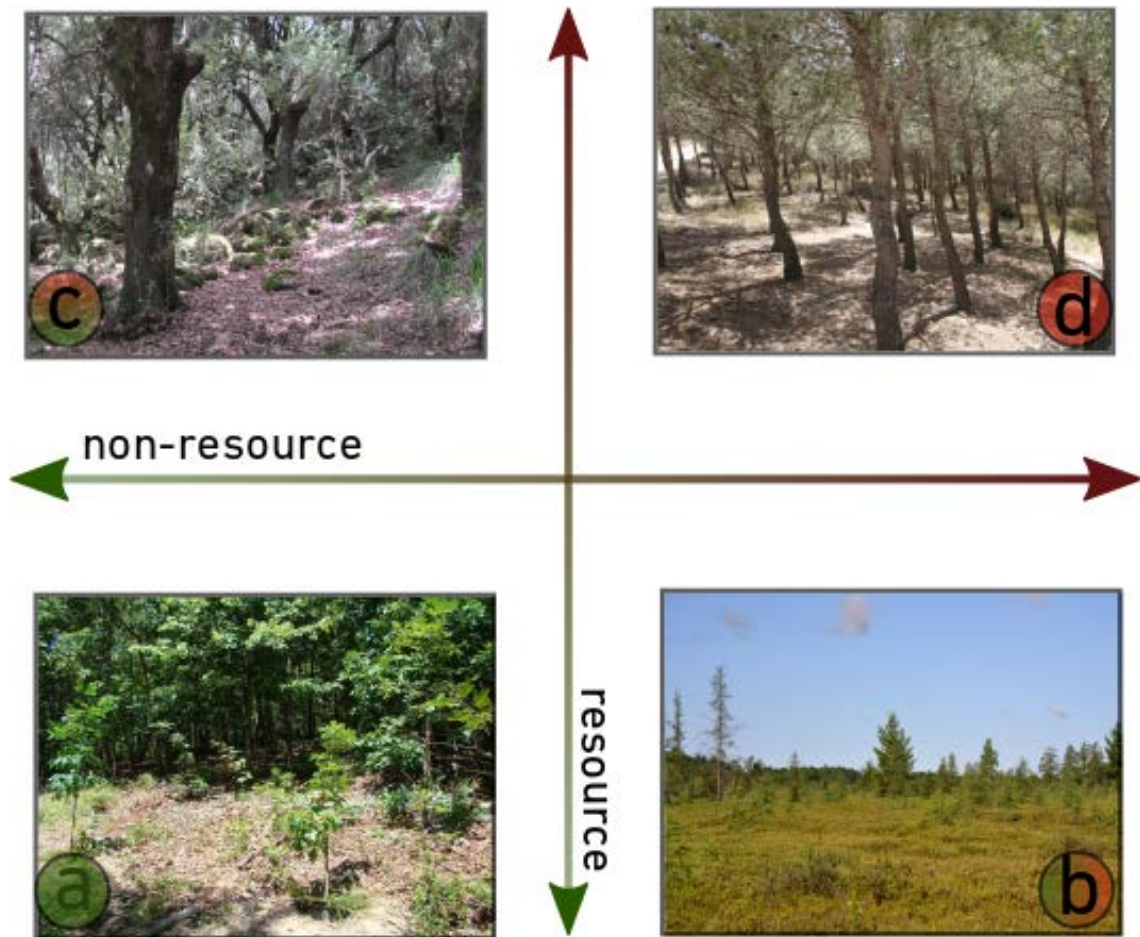
FIGURE 6.1: A two dimensional environmental gradient. In this example, the non-resource factor is soil ph, and the resource factor is available direct sunlight. Considering a plant species with optimal fitness at basic ph levels and high levels of direct sunlight, the environmental gradients show different combinations of factors: (a) suitable light and ph levels may be found in open areas or forest gaps on basic soils, (b) peat bogs are highly acidic environments, but otherwise suitable regarding light levels, (c) closed canopies under basic soils may have too low light levels, (d) understoreys of pine forests have both low light levels and acidic soils.

6.2 Methods

Modelling community responses to a combined gradient

The basic tenets presented above apply, all else being equal, to gradients of only one factor at a time. However, it is harder to derive conceptual predictions about variations across combined gradients of both types. Using a simple community model, we analysed whether variations in two environmental factors, a resource and a non-resource one, drive variations in different patterns of a horizontal

community (composed of a single trophic guild). We generated a pool of species with varying demographic responses to non-resource stress factors, following the functional responses discussed in Maestre et al. (2009), in which species vary their survival and growth rates according to the level of non-resource stress (Appendix 6.1). The two extreme cases in this framework are, on the one hand, stress-tolerant species, that are able to maintain comparatively high survival rates under high stress levels, but display lower growth rates in the absence of stress; and competitive species on the other hand, that show high growth rates under benign conditions but also higher sensitivity in both survival and growth rates to non-resource stress.

In our model setting, environmental variability is represented by a two-dimensional lattice, in which each cell has a combination of resource and non-resource environmental factors (Fig. A.6.1.1). The resource factor is represented as the carrying capacity of the cell, and all species are assumed to belong to the same trophic guild (sensu Fauth et al. 1996), whose only limiting factor is that resource. The non-resource factor is homogeneous and constant in a given cell. Both gradients are linear.

Species randomly colonize with equal probability any given cell of the lattice, and survive and grow according to their specific functional responses (Fig. A.6.1.2). A fraction of species is able to facilitate the survival of heterospecifics, by enhancing their survival probability in the face of high levels of non-resource stress. The intensity of each facilitation event is given by the biomass of the benefited individual, that would have otherwise not survived.

Individuals in a cell are able to grow up to the level where their aggregated biomass equals the carrying capacity of the cell, i.e. the level of resource factor. Competition occurs when the growth of one or more individuals is hampered due to the presence of another individual, and its intensity is given by the amount of expected growth that was impeded by the competitive exclusion.

With this simple setting, we modelled how species interact and persist through time in each combination of the two gradients. After an initial warm-up period of 100 timesteps, to allow each cell to be colonised, we recorded for 500 timesteps every facilitative and competitive interaction, the effective number of species at each cell (also known as "Hill number" or "true diversity", Tuomisto 2012), and the average persistence time of species at each cell. To evaluate the response of these metrics to the environmental gradients, we fitted generalised additive models (GAMs) to the results from our simulations. Generalised additive models use smoothing functions to model nonlinear relationships, providing a flexible nonparametric model (Wood, 2017). Given the strong nonlinearities observed in our responses, we fitted GAMs with adaptive smoothing terms, that are able to model responses where the degree of smoothness vary over the range of the covariates (Wood, 2017).

We also performed simulations with the same parameterization but not allowing for facilitation, and compared the distributions of competition intensity, species diversity, and persistence times in the two sets of simulations, using Wilcoxon signed-rank tests.

6.3 Results

Does the intensity of competitive and facilitative interactions vary across a combined resource and non-resource environmental gradient?

The intensity of competition and facilitation strongly varies across the combined environmental gradient (Fig. 6.2, Table 6.1). Competition intensity increases with increasing resource stress (Fig. 6.2, panel a) and with decreasing non-resource stress (Fig. 6.2, panel b), and the interaction between resource and non-resource stress is also statistically significant (Table 6.1). Facilitation intensity, in turn, is only significantly influenced by non-resource stress (Table 6.1, Fig. 6.2, panel c and d). In absence of stress, there is no facilitation, as every species has a survival probability of 1 (Fig. A.6.1.2). Then, as non-resource stress increases, facilitation intensity displays a concave parabolic shape: it is high and very variable for low levels of stress, lowest for intermediate levels, and consistently high and comparatively less variable for high stress levels.

Table 6.1: Results of the Generalised Additive Models fitted to the simulation results. REML = Restricted maximum likelihood. For parametric coefficients, their estimates, standard errors, and t-statistic are given, whereas for smooth terms, we report their estimated degrees of freedom (edf), and their F-statistic.

Response	REML	r^2	Deviance	Covariates	Estimate	Std.Error	t	edf	F	p-value
facilitation intensity	-1376.2	0.528	53.1%	intercept	0.674	$6.3 * 10^{-3}$	106.56	-	-	< 0.05
				resource	$-4.8 * 10^{-5}$	$1 * 10^{-4}$	-0.465	-	-	0.642
				s(non-resource)	-	-	-	14.16	167.5	< 0.05
competition intensity	-5459.3	0.967	96.7%	intercept	0.108	$5.2 * 10^{-4}$	208.4	-	-	< 0.05
				s(resource)	-	-	-	3.28	7405	< 0.05
				s(non-resource)	-	-	-	12.53	1813.5	< 0.05
				s(resource*non-resource)	-	-	-	25	262.4	< 0.05
persistence times	7451.8	0.986	98.6%	intercept	26.18	0.217	120.71	-	-	< 0.05
				resource	$2.2 * 10^{-3}$	$3.5 * 10^{-3}$	-0.625	-	-	0.532
				s(non-resource)	-	-	-	14.29	10741	< 0.05
effective number of species	4127.2	0.922	92.2%	intercept	4.828	0.057	83.92	-	-	< 0.05
				resource	-0.016	$9.4 * 10^{-4}$	-16.64	-	-	< 0.05
				s(non-resource)	-	-	-	10.36	2355	< 0.05

Table 6.2: Results of the Wilcoxon signed-rank tests for differences in competition intensity, species diversity, and average persistence times between communities with and without facilitation. Test on competition intensity is two-tailed, reflecting our lack of previous hypotheses on the intensity of competitive effects between the two sets of simulations. Tests on species diversity and persistence are one-tailed, with the alternative hypothesis being greater values of both metrics when facilitation is allowed. In bold, highest median values of each quantity.

	median - facilitation	median - no facilitation	V	p-value
competition intensity	**0.059**	0.050	1229233	< 0.05
persistence time	**15.47**	12.369	2401500	< 0.05
effective number of species	**2.374**	2.067	2600200	< 0.05

How are species diversity and persistence affected by the environmental variation?

The effective number of species at each cell drops rapidly with even slight increases in non-resource stress (Fig. 6.2, panel f), and also shows a decreasing trend, although less steep, with increasing resource stress (Fig. 6.2, panel e). Average persistence time, in turn, also decreases very sharply with non-resource stress (Fig. 6.2, panel h), but is unaffected by resource stress (table 6.1, Fig. 6.2, panel g).

Does the presence of benefactor species increase species diversity and persistence in our model communities?

Both species diversity and persistence times are significantly higher in simulations with facilitation (Table 6.2, Fig. A.6.1.4).
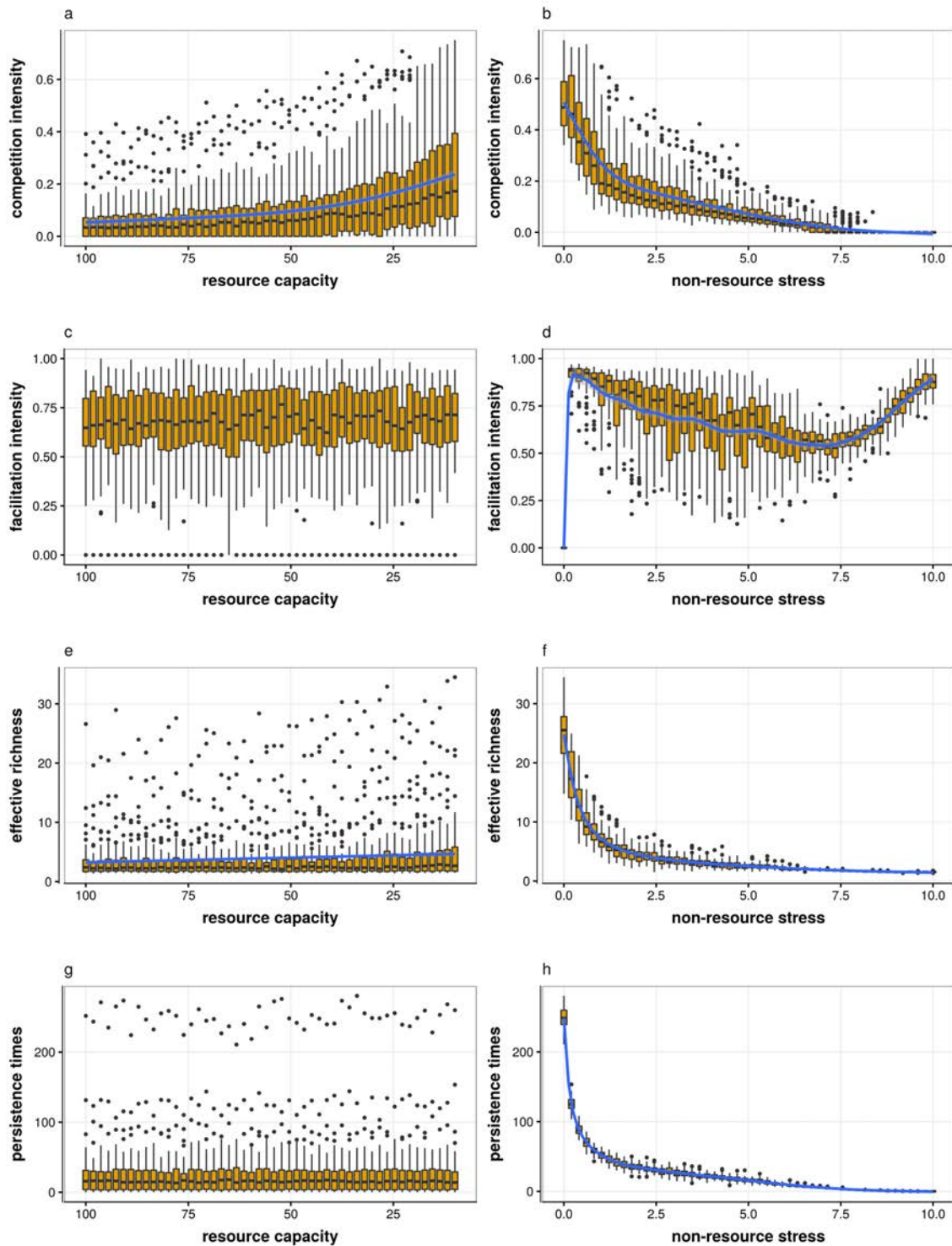
Figure 6.2: Variation of community-level properties across a resource and a non-resource gradient. For variables selected as significant by the GAM models (Table 6.1), model fits are superimposed as blue curves.

6.4   Discussion

We modelled the response of species ranging from pure competitors to pure stress-tolerance within a two-dimensional environmental gradient combining a resource and non-resource factor. The two types of environmental factors have contrasting influences on (1) the intensity of pairwise interactions and (2) the diversity of species in the community and their average persistence times.

The intensity of competitive interactions clearly increases with increasing levels of resource stress, as expected. However, it also increases for decreasing levels of non-resource stress. This is due to the positive correlation observed between mortality rates and non-resource stress, that releases resources and decreases effective competition at highly stressful environments.

Facilitation is, again as we hypothesised, clearly driven by variations in the non-resource factor. The response observed is, however, more complex than the standard expectations derived from the stress-gradient hypothesis, that predicts either an increasing importance of facilitation with increasing stress, or an increase followed by a collapse in facilitation levels at very high stress levels (le Roux and McGeoch, 2010). The idea behind this latter version of the theory is that in extremely harsh environments, the facilitation effect of nurse plants is severely hampered (Michalet et al., 2006). This reasoning, however, only applies to non-resource factors, as species do not compete for them; if the environmental gradient includes resource factors, net interaction effect may switch from positive to neutral or negative (Smit et al., 2007; Michalet et al., 2014). In our simulations, we first observed, as expected, no facilitation in the absence of non-resource stress. As soon as there is a certain environmental impact on competitive species, however, facilitation sharply increases, while at the same time showing a high variability. We argue that this unexpected variability is due to priority effects, in which the order of arrival of species to a location is an important factor for the subsequent dynamics of the local community (Fukami, 2015). In our model, all species have the same probability of colonizing any cell of the grid: if the first colonizers are facilitators, follow-up colonizers will likely experience some degree of facilitation as long as stress levels are not null. On the other hand, facilitation will be residual if the early colonizers are able to thrive in the location but do not facilitate the establishment of other species. Following the environmental gradient, If non-resource stress increases, stress-tolerant species will be progressively selected for, and competitive species will only persist when facilitators are present. At very high stress levels, survival probability is extremely low for all species, so most surviving individuals are subject to a certain degree of facilitation. It is important to note that, in our model, facilitation capacity does not decrease with increasing stress, as may occur for example in grazing gradients (Smit et al., 2007). We also note that we explicitly modelled locations with unlimited potential colonizers from the same regional species pool, in order to isolate effects arising directly from environmental constraints on response curves, and discard species-pool effects (e.g. Pärtel et al. 1996).

In this first approximation to the concurrent modelling of resource and non-resource environmental gradients, we defined a single resource factor as a carrying capacity, and did not account for more complex relationships that allow facilita-

tion of resource factors. For example, it is well established that, although species compete for water in stressful environments, nurse species can facilitate water acquisition by heterospecifics under different circumstances, listed in Maestre et al. (2009): by lifting water from belowground, by providing shade that retains moisture, and, again as a byproduct of shade provision, by modifying water-relations of the understorey species. Aside from the important example of water, it is nevertheless clear that most resource factors shared by species of a certain guild (i.e. light, space, nutrients) are generally not facilitated by species of that guild, and hence the prevalence and intensity of facilitation should, in most cases, conform to the hypothesis laid out here.

Species diversity and persistence are highly sensitive to variations in the non-resource factor, and this is mainly due to the shape of the physiological responses to non-resource stress that we modelled (Fig. A.6.1.2). Less steep declines in survival or growth probability would smooth the responses to increasing stress. We carried out additional simulations (not shown here) and observed that higher variation between purely competitive and purely stress-tolerant species did indeed increase the steepness of the diversity and persistence responses. Nevertheless, the overall trends were qualitatively robust to the different parameterizations, and should hold as long as competitive species are comparatively more sensitive to stress.

Despite facilitation being present at high levels of non-resource stress, species diversity and persistence time both decrease consistently across the non-resource gradient: the negative effects on growth and survival across the species pool are stronger than the benefits of facilitation by stress-tolerant species. Facilitation does, however, increase competition intensity, species diversity and persistence times overall (Table 6.2), with its strongest influence occurring at low to moderate levels of non-resource stress (Fig. A.6.1.4).

In our model, we considered a single non-resource environmental factor and a single resource that is utilised equally by all species and does not deplete. Of course, the picture is much more complex in natural systems, where species consume several resources with varying efficiencies (Chapin et al., 1987) and may display contrasting physiological response curves to different non-resource factors (Austin and Gaywood, 1994). Furthermore, we are considering here horizontal communities, and the responses discussed will likely be more complex for multi-trophic communities and involve direct and indirect effects on community properties (Menge and Sutherland, 1987; Bruno et al., 2003). We expect that in communities comprising several guilds and potentially different types of interactions among species, variations in non-resource factors will (1) directly affect all species regardless of their position in the community, and (2) those effects will not be homogeneous. In particular, it is expected that species up in the trophic chain will be comparatively more sensitive to environmental variability (Voigt et al., 2003). Therefore, as a first hypothesis, we suggest that non-resource environmental gradients will trigger both direct effects on all trophic guilds and also significant top-down indirect effects on community structure and dynamics. In turn, variations in resource factors can be expected to affect more significantly lower trophic levels, since species of higher trophic levels get most of their nutrients from direct consumption of organic matter from lower trophic levels. As

such, we hypothesize that the most important effect on community structure and dynamics across non-resource environmental gradients will be through bottom-up control.

Despite the simplicity of our model, we have clearly shown that the two general types of resource and non-resource environmental factors differentially influence biotic interactions, species richness and persistence in model communities. Several fundamental questions arise from these results. The spatial scale of different environmental gradients, for example, should interact with the spatial signal of the different interaction types (Araújo and Rozenfeld, 2014) to influence large-scale persistence and diversity patterns. Even at local scales, integrating the different aspects of environmental variability with established frameworks such as the resource ratio theory or modern coexistence theory should bring novel insights for the influence of environmental gradients on ecological communities.

General discussion and conclusions 7

We live in a time in which global environmental changes are occurring at unprecedented scales and speeds (Pachauri et al., 2015). Individual species and whole ecological assemblages face systemic risks from a variety of stressors, including the loss and fragmentation of suitable habitat, alterations in the temperature and precipitation regimes, pollution, or an increase in the rate of colonization of human-borne potentially invasive species (Vitousek, 1994). Given the scale and magnitude of the human alteration of the environment, it is urgent to develop mitigating measures at all levels, from actions in local habitats to coordinated worldwide socioeconomic efforts that bring us closer to a harmonious coexistence with the non-human world. In order to move towards this admittedly utopian objective, we need the strongest possible scientific understanding of how ecological species and communities are structured, and how they function. In a testimony to the complexity of the natural world, our knowledge of ecological communities is still limited, despite decades of continued work by generations of naturalists and ecologists. In particular, we do not know whether pairwise interactions between individuals are structured in order to enhance community stability sensu lato. When certain interactions are considered in isolation, e.g. trophic or mutualistic ones, theoretical (Williams and Martinez, 2000) and empirical (Thébault and Fontaine, 2010) studies have shown that interactions are indeed distributed non-randomly. However, species in ecological communities display a wide array of interaction types and mechanisms, and we are only starting to gain a broad understanding of how the different interactions combine in natural systems (Kéfi et al., 2015), and its implications for ecological processes (Pocock et al., 2012).

In this thesis, I have explored several fundamental questions about networks of ecological interactions, their structure and dynamics in different contexts. In the following paragraphs, I discuss some of the main findings of the thesis and potential lines of work arising from them, in light of the current literature knowledge.

There are only a handful of empirical datasets that account for multiple interaction types in ecological communities (chapter 2). It is therefore only logical that most studies that analyse these complex networks are theoretical in nature, but even restricting ourselves to theoretical models for building and analyzing multiple interactions networks, the diversity of approaches and objectives is already substantial. I have shown that, on a conceptual level, this diversity of modelling strategies boils down to three types of approaches (chapter 2). This conceptualization may help researchers design theoretical studies with a clearer understanding of the limitations and strengths of the methodologies used. For example, not all interaction types occur in the same spatial and temporal scales. Models that lump together interaction effects in a single parameter and do not differentiate spatiotemporal patterns (such as the model developed in chapter 3) should be very explicit about these limitations, and in any case, should be considered baseline models, potentially useful for (1) guide further, more targeted theoretical and empirical work, and (2) comparison against more realistic models. Looking at the broad picture, one may ask whether the increase in model complexity and data collection programs necessary for accounting for different interaction types is worth it, i.e. if it significantly improves our understanding of ecological communities. Although the field is still young, and all conclusions are based on highly idealized

models or on very specific, likely incomplete datasets, current results suggest that, indeed, integrating the variety of interactions present in nature into the study of ecological networks produces novel insights and unexpected outcomes, regarding for example the patterns of secondary extinctions in networks (Pocock et al., 2012; Evans et al., 2013), the functional groupings in communities (Kéfi et al., 2016), or, as shown in chapter 3, the persistence of species in their local communities. It remains to be seen, however, if a truly consistent program of data collection across different community types and environmental gradients is feasible, or how more modest experiments such as microcosms can be designed for taking full advantage of this view of ecological communities.

As stated above, before we can extract robust conclusions from empirical data, we may advance our understanding of multiple interaction networks by developing general, overarching models and theories. With that objective in mind, I developed the model of chapter 3, and in its design, I brought together a series of separate insights about interaction networks. In particular, the way in which interactions are quantified is based on the assumption that the abundance of the interacting species is related to their interaction frequency: the more abundant the two species are, the more will they interact. Interaction frequency is, in turn, taken as a measure of the impact of one species over another. This assumption has been corroborated for a number of plant-pollination networks (Vázquez et al., 2005, 2007, 2012), but it probably does not hold generally for all interaction types, and it explicitly neglects specialization in ecological interactions. Nevertheless, it represents a robust approach for integrating with a single currency the effects of disparate interaction types in dynamic models.

The results from chapter 3 open different avenues for future research. The most straightforward extension would be the development of experimental or observational studies for testing some of the results: in particular, it would be feasible to test whether species-poor communities tend to have a higher prevalence of positive interactions, as suggested by our theoretical results, and how are these interactions distributed. The assumption that interactions are distributed non-randomly proved key for maintaining high levels of persistence: even in species-poor communities, interactions should maintain a certain structure. Such targeted empirical work could also start to unveil the frequency and structure of less studied interactions. Amensalism and commensalism have been shown in another recent study to improve community stability when accounted for (Mougi, 2016*a*), but they are clearly underrepresented in the literature. Another theoretical outcome from that chapter that would require further study is the observed relationship between the frequency of occurrence of the different interaction types and their connectance values (Appendix 3.4). As long as the set of feasible potential links varies for the different types of interaction, frequency of occurrence and connectance will not be equivalent. I believe that the calculation of connectance relative to fully connected networks should be approached with caution, as there are countless examples in which many of the potential interactions are forbidden because of, for example, non-overlapping activity in time or space (Yang and Rudolf, 2010; Osorio et al., 2018). In any case, it is unlikely that in multitrophic networks, the set of, say, potential mutualisms, would be the whole network. When evaluating more thoroughly structural metrics of multiple interactions

networks, these details should not be overlooked. Note that, throughout chapter 3, I have purposely concentrated on species abundances and already established interactions. Trait-based approaches for inferring interactions (Morales-Castilla et al., 2015; Bartomeus et al., 2016) and community structure (Laigle et al., 2018) also show great promise, but they are difficult to generalize to different types of communities and habitats. It is probably not possible to derive a set of traits from which to predict the occurrence of different interactions, applicable across trophic levels and habitat types. But perhaps it is feasible to ask whether, in a general way, traits that are known to influence trophic interactions are also important in mediating other interaction types (e.g. are species of similar body sizes more likely to compete with each other?).

The only "trait" included in the model of chapter 3 is the trophic level of each species. From this separation of species into trophic levels, I found that the persistence values in different trophic levels were markedly different in the simulated communities (Fig. A.3.2.1). This result prompted the question that would end up shaping chapter 4: if persistence levels in complex communities are affected by interaction type frequencies and network structure, other community-level patterns should also be affected. This question points to a more general feature of ecological thinking, discussed in chapter 4. Community ecology has, historically and for several reasons, concerned itself with communities of a single functional guild, whereas analyses of ecological networks followed a parallel path in which functional distinction among species is assumed seamlessly. Many highly influential theories in community ecology have been framed in terms of competition for resources within a certain guild (e.g. Tilman's resource ratio theory, Chesson's modern coexistence theory), and only recently the frame is expanding in order to account for interactions among functional guilds (Chesson and Kuang, 2008; Godoy et al., 2018; Seibold et al., 2018). An implicit objective of chapter 4 was to advance in this expansion of classic community ecology patterns into multi-trophic communities with potentially complex network structures. The most important message from chapter 4 is that context matter, and many factors interact when trying to elaborate how patterns vary across trophic guilds. We are not yet even close to a conceptual theory of community ecology of complex ecological networks, but this and the aforementioned studies are steps towards that goal.

In chapter 5, I delved deeper in that overarching objective of advancing community ecology for multi-trophic communities, this time focusing on the spatial dimension of interactions. Metacommunity theory has provided very important insights in the functioning and dynamics of spatially-connected communities. Again, most of this framework has revolved around two key assumptions: communities are horizontal, comprised of a single guild of species that compete among them, and these discrete communities are conected by dispersing individuals. After almost two decades of work, recent studies started to expand the paradigm of metacommunity ecology in different ways, e.g. considering more complex communities or integrating different forms of individual and material connections between communities. We opted for combining both extensions to classic metacommunity theory, and found that, as could be intuitively expected, when species forage into different patches, interaction dynamics clearly differ from the

dispersal case. Spatial effects are propagated generally up to four or five links in the metacommunities of our general model, an insight that, if it holds, could have conservation implications for instance for evaluating the regional impact of species introduced in a limited number of localities.

Arising from the model of chapter 3, a prominent question we faced was how could we generate frequencies and topologies of interaction types that were realistic, or at least approaching some degree of realism. We ended up doing a literature review on how the different interaction types occurred across different trophic levels, but this is only an ad-hoc solution for that particular study. In order for studies on multiple interactions to advance, robust knowledge on the frequency and topology of different interactions across environmental gradients and community types is sorely needed. This prompted the research of chapter 6, which matured in a fairly different way from that original idea. Originally, we expected to generate predictions of interaction frequencies in communities based on environmental or other constraints (imagine a world map with regions differentiated by the prevalence of the different interaction types, e.g. mutualism-dominated communities or predation-dominated ones). This, however, proved too demanding given the limited time frame of a Ph.D. project and the absolute lack of data. I resorted to study horizontal communities, and quite early realized what is now the core idea from chapter 6: that environmental factors are very different from one another and this differentiation should be better reflected in studies of ecological patterns across gradients. In that chapter, I only hint at what the effects of different gradients could trigger in more complex communities, but this line of research is potentially among the most important ones arising from the Ph.D.

A common theme to all chapters is the reliance on simulation methodologies to infer ecological insights applicable beyond the simple systems modelled. Numerical simulations allow a greater degree of model flexibility and complexity than analytical derivations, but of course it is harder to pinpoint the importance of the different model parameters, given their higher number and the difficulty of performing exhaustive sensitivity analyses. An important strength of simulation methods is that they allow the explicit inclusion of stochasticity on the model system, as I have tried to include in all the models developed. Interactions and functional relations in ecological communities are probabilistic in nature, rather than fixed, and I tried to keep that in mind in all the outcomes of the thesis. Given the nature of the questions asked in this thesis, I was not able to test most of the theoretical predictions against empirical data. This divide between theory and empiricism is a long-standing problem in ecology, perhaps more so than in other disciplines, and is discussed in detail in each chapter. It was my intention, however, to develop theoretical models with an eye on potential follow-up tests in natural systems. Therefore, in the following section, I advance in more detail how the chapters in this thesis could be complemented by experimental or observational studies.

Empirical observations, experiments, and applications

The adequate sampling of ecological networks is a key issue in community ecology (Jordano, 2016), with important consequences for assessing the functional role of

species within a network or the relative prevalence of rare and weakly-interacting species. In chapter 2, we discuss the main strategies employed so far for collating networks with multiple interaction types. These can be summarized as follows: a first alternative is to join together data from different sources and generate an inferred network; a second alternative is to develop comprehensive sampling programs of different functional groups and interaction types of specific communities. In both cases, the conceptual and logistic problems are potentially important. For example, when mixing data from different sources, one must make sure that there are no biases associated with the spatiotemporal extent of the sampling, or at least, incorporate these dimensions in the analysis (see chapter 4). This is particularly important for functional groups which are likely to have very different home ranges and dispersal distances.

Perhaps the most straightforward way of sampling complete networks is to resort to artificial mesocosms or natural communities with relatively few species or interactions (e.g. the Aire Island in chapter 2, or the core interactions in a mediterranean forest community studied by Sunyer et al. 2016). However, in all these scenarios there remains the issue of correctly documenting and quantifying direct interactions of different types, a discussion that has developed independently in food web studies (Berlow et al., 2004; Wootton and Emmerson, 2005; Novak and Wootton, 2010), networks of competitive interactions within a single trophic level (Freckleton et al., 2009; Hart et al., 2018), and mutualistic networks, mainly plant-pollinator ones (Vázquez et al., 2005, 2007; Holland et al., 2002). Virtually no empirical study that I am aware of has quantified the importance of one-way interactions (amensalism and commensalism) or has compared the relative importance of different interaction types in a single multi-trophic community, although recent calls for integrating multi-trophic approaches in community ecology are appearing: alongside this thesis, see for example Seibold et al. (2018). An adequate sampling, in communities across environmental gradients, of (1) abundances and traits such as body size of species from key functional guilds, including parasites/parasitoids (Lafferty et al., 2006), (2) interaction frequencies and/or per capita strengths, is the golden standard to which we should move forward. Such data, when appropriately replicated, could easily corroborate or refute many of the ideas presented in chapters 2, 3, 4, and 6 of this thesis. As stated above, one way to approach this challenging program is through the use of artificial mesocosms, which allow the deployment of many types of experimental designs with appropriate control types, for example varying environmental or nutrient-input gradients (Moss et al., 2004), community assembly (Chase, 2007; Jiang and Patel, 2008), or colonization rates (Fahimipour and Hein, 2014). By establishing pond mesocosms along, for example, a warming gradient and a complementary nutrient-input gradient, the effects of the environment on interaction importance could be measured (chapter 6), and the short-term persistence of species (chapter 3) as well as the distribution of abundances of the different trophic guilds (chapter 4) could be quantified.

The spatial propagation of interactions in metacommunities connected by dispersal and foraging would require slightly more elaborate experimental designs. In particular, foraging requires species dwelling at a reproductive site that eventually move to feed in other localities. In order to test the differential effects of

a foraging species in its home location and in other local communities, long-term experiments relative to the generation times of the species should be set up, and if artificial mesocosms were to be used, the different localities should be connected by a matrix allowing movement at least in a linear fashion. Furthermore, local communities should be set so as to prevent the establishment of the forager species in sites other than its home site. For example, predatory fish with specific needs for their reproductive sites could be introduced in mesocosms engineered with the appropriate characteristics for their breeding, while at the same time connecting these home mesocosms to other ones in which fish could eventually forage but not breed.

All these proposals are at this moment speculative, but feasible given appropriate projects and time frames. In the more general topic of how the insights from this thesis and its potential follow-ups could benefit applied ecology, it is relevant to note that the spatial scales in which ecologists define ecological communities and metacommunities are coherent with the scales at which local conservation and restoration projects are carried out. For example, quoting Wainwright et al. (2017): "Community ecology theory has particular relevance to restoration because it describes the processes that underlie the assembly, maintenance of diversity and functioning of ecological communities, which are often the focus of restoration projects".

Insights on species persistence (chapter 3), the distribution of species abundances (chapter 4) and their spatiotemporal variation are key for preserving ecosystem functioning and diversity. In particular, a network perspective to conservation and restoration ecology is urgently needed. As Harvey et al. (2017) notes, species interactions must be taken into account when assessing conservation priorities, due to the interdependencies and feedbacks that arise from direct and indirect interactions. Often, as it has been shown previously (Menge, 1995; Suttle et al., 2007; Montoya et al., 2009) and in chapter 5 of this thesis, the net effect of interactions can reverse the expectations from direct interactions or from environmental constraints. Thus, preserving interactions appears to be as important as preserving keystone species, in order to maintain both community structure and function (Wang and Brose, 2018). In turn, the variability of interaction occurrence and outcome along environmental gradients is still hardly known (Poisot et al., 2017), and more empirical work is necessary on a variety of systems and interactions.

Throughout this thesis, I have stated the need for more directed, long-term empirical efforts in order to improve our basic knowledge of ecological communities and their mechanisms. Maintaining a balance and a healthy dialogue between theoretical research and applied ecology is by all means necessary if we are to help mitigate the current biodiversity crisis. Hopefully this thesis will contribute to that objective.

Conclusions

- **Chapter 2:**

    - There is a high diversity of objectives and methodologies for studying

ecological networks with multiple interaction types. Despite this variability, most theoretical approaches can be reduced to three conceptual methodologies. Multilayer networks are the most general one, and the other two methodologies can be seen as special cases of multilayer networks, that focus on different aspects of the interaction network.

– The three methodologies proposed are best suited to different types of interaction data, and to different objectives. The single most important issue we face in the study of multiple interactions networks is the lack of robust data for a variety of communities and habitat types.

- **Chapter 3:**

  – In model communities, species persistence is highly influenced by the frequency and distribution of interaction types. In particular, the prevalence of positive interactions is significantly related to persistence in species-poor communities. In richer communities, this relationship is diluted, and different combinations of interaction frequencies are able to maintain high levels of persistence.

  – Structural properties of the model networks are also important for species persistence, in the sense that more structured communities are more persistent. Furthermore, the simulated communities display emergent structural properties also found in empirical food webs.

- **Chapter 4:**

  – The distribution of abundances varies between guilds of terrestrial plants and mammals. In particular, abundances of terrestrial plants tend to be significantly less even and more skewed than those of mammals. Variations in competitive exclusion among guilds due to differences in niche availability may partly explain these trends.

  – The patterns among consumer guilds are qualitatively similar to those predicted by simple theoretical models, and are mediated by other interacting factors such as the richness of the guild under study, the temporal and the spatial extent of the data acquisition scheme.

- **Chapter 5:**

  – The spatial propagation of interaction effects across local communities has a different signature depending on whether localities are connected by dispersing or foraging organisms. When local communities are connected by foraging, the net effects between any pair of species are much less predictable from local dynamics than in the dispersal case.

  – The spatial decay of interaction effects follows a similar curve regardless of the type of movement between communities. Most interactions have a net effect on species up to five links away from the interacting pair, but rarely more.

- **Chapter 6:**

– Environmental factors have different effects on species dynamics and interactions depending on whether they are consumed by species (resource factors) or not (non-resource factors). In particular, variations in non-resource factors drive gradients in facilitation intensity, whereas resource factors are the main driver of gradients in competition intensity. Other properties at the community level are also affected by these environmental gradients: species diversity and persistence times are mainly driven by variations in non-resource factors, with small effects from resource factors.

– The distinction between resource and non-resource factors is likely to be even more important for communities with several functional or trophic guids, as different factors affect differentialy the different guilds and potentially generate complex bottom-up and/or top-down dynamics.

Appendix 2.1: Chapter 2 - Case study model parameterizations and procedure

Expanded Food Web

The model is of the form:

$$\frac{dN_x}{dt} = r_x N_x - m_x N_x^2 + \sum_{y \in S, y \neq x} a_{xy} N_x N_y \tag{7.1}$$

where S is the set of species. Non-trophic interactions (NTI) may affect the growth rate r_x, mortality rate m_x or interaction strength a_{xy} terms. The ones included in our model are, respectively:

growth rates

$$r_{CM} = \frac{r_{CM}^{NTI} N_{PL} + r_{CM}^0 N_{PL}^0}{N_{PL} + N_{PL}^0} \tag{7.2}$$

$$r_{DP} = \frac{r_{DP}^{NTI} N_{HM} + r_{DP}^0 N_{HM}^0}{N_{HM} + N_{HM}^0} \tag{7.3}$$

$$r_{PL} = \frac{r_{PL}^{NTI}(N_{CM} + N_{HM} + N_{PLe}) + r_{PL}^0(N_{CM}^0 + N_{HM}^0 + N_{PLe}^0)}{(N_{CM} + N_{HM} + N_{PLe}) + (N_{CM}^0 + N_{HM}^0 + N_{PLe}^0)} \tag{7.4}$$

$$r_{PLe} = \frac{r_{PLe}^{NTI} N_{PL} + r_{PLe}^0 N_{PL}^0}{N_{PL} + N_{PL}^0} \tag{7.5}$$

mortality rates

$$m_{HM} = \frac{m_{HM}^{NTI} N_{SV} + m_{HM}^0 N_{SV}^0}{N_{SV} + N_{SV}^0} \tag{7.6}$$

interaction terms

$$a_{PL,DP} = \frac{a^{NTI}_{PL,DP} N_{HM} + a^0_{PL,DP} N^0_{HM}}{N_{HM} + N^0_{HM}} \tag{7.7}$$

$$a_{DP,PL} = \frac{a^{NTI}_{DP,PL} N_{HM} + a^0_{DP,PL} N^0_{HM}}{N_{HM} + N^0_{HM}} \tag{7.8}$$

We performed two sets of simulations, with and without non-trophic interactions (NTI henceforth). In the simulation without NTI, we assumed that *Podarcis lilfordi* (PL) consumed seeds of *Helicodiceros muscivorus* (HM), *Pistacia lentiscus* (Ple) and *Chritmum maritimum* (CM); these interactions were modelled as mutualisms in the NTI simulation, with the presence of PL individuals increasing the growth rate of each associated plant species. Each simulation was replicated 100000 times for 2500 timesteps. In the main text we report the aggregated results of the 100000 replicates. Each parameter was assigned a minimum and maximum value, and in each replicate parameter values were taken randomly from these intervals.

Parameter ranges for the simulation without NTIs:

Growth and mortality rates:

$r_{FT} = [-0.01, -0.001]$

$r_{PL} = [0.01, 0.1]$

$r_{DP} = [0.4, 0.6]$

$r_{SV} = [0.05, 0.15]$

$r_{HM} = [0.15, 0.25]$

$r_{PLe} = [0.05, 0.15]$

$r_{CM} = [0.15, 0.25]$

$m_{FT} = [0.0001, 0.0015]$

$m_{PL} = [0.0001, 0.0015]$

$m_{DP} = [0.0005, 0.0015]$

$m_{SV} = [0.0005, 0.0015]$

$m_{HM} = [0.0005, 0.0015]$

$m_{PLe} = [0.0002, 0.0004]$

$m_{CM} = [0.00005, 0.00015]$

Interaction coefficients $\neq 0$:

$$a_{FT,PL} = [10^{-6}, 10^{-4}]$$
$$a_{PL,FT} = [-10^{-2}, -10^{-4}]$$
$$a_{PL,DP} = [10^{-4}, 10^{-2}]$$
$$a_{PL,HM} = [10^{-6}, 10^{-4}]$$
$$a_{PL,PLe} = [10^{-7}, 10^{-5}]$$
$$a_{PL,CM} = [10^{-7}, 10^{-5}]$$
$$a_{DP,PL} = [-10^{-5}, -10^{-7}]$$
$$a_{DP,HM} = [10^{-6}, 10^{-4}]$$
$$a_{HM,PL} = [-10^{-6}, -10^{-8}]$$
$$a_{HM,DP} = [-10^{-6}, -10^{-8}]$$
$$a_{PLe,PL} = [-10^{-6}, -10^{-8}]$$
$$a_{CM,PL} = [-10^{-6}, -10^{-8}]$$

Initial abundances:

$$N_{FT} = 8$$
$$N_{PL} = 5000$$
$$N_{DP} = 200$$
$$N_{SV} = 5000$$
$$N_{HM} = 5000$$
$$N_{PLe} = 200$$
$$N_{CM} = 5000$$

Parameter ranges for the simulation with NTIs. Parameters without superscript are not affected by NTIs. Parameters with superscript 0 indicate values in the absence of NTI, i.e. when one of the interacting species is not present. Parameters with superscript NTI indicate the maximum value that the parameter can reach with NTI:

$$r_{FT} = [-0.01, -0.001]$$
$$r_{PL}^0 = [0.01, 0.1]$$
$$r_{PL}^{NTI} = [0.15, 0.25]$$
$$r_{DP}^0 = [0.65, 0.75]$$
$$r_{DP}^{NTI} = [0.4, 0.6]$$
$$r_{SV} = [0.05, 0.15]$$
$$r_{HM}^0 = [0.15, 0.25]$$
$$r_{HM}^{NTI} = [0.45, 0.55]$$
$$r_{PLe}^0 = [0.05, 0.15]$$
$$r_{PLe}^{NTI} = [0.15, 0.25]$$
$$r_{CM}^0 = [0.15, 0.25]$$
$$r_{CM}^N TI = [0.35, 0.45]$$
$$m_{FT} = [0.0001, 0.0015]$$
$$m_{PL} = [0.0001, 0.0015]$$
$$m_{DP} = [0.0005, 0.0015]$$
$$m_{SV} = [0.0005, 0.0015]$$
$$m_{HM}^0 = [0.0005, 0.0015]$$
$$m_{HM}^N TI = [0.00005, 0.00015]$$
$$m_{PLe} = [0.0002, 0.0004]$$
$$m_{CM} = [0.00005, 0.00015]$$

In this simulation, only the interactions PL-DP and FT-PL are considered trophic. Therefore, we report only *a* values for these. The FT-PL interaction is not affected by any third species, but the PL-DP interaction is mediated by the presence of HM plants: a higher abundance of HM flowers increases the probabilities that an interaction takes place, therefore increasing its net outcome.

$$a_{FT,PL} = [10^{-6}, 10^{-4}]$$
$$a_{PL,FT} = [-10^{-2}, -10^{-4}]$$
$$a_{PL,DP}^0 = [10^{-7}, 10^{-5}]$$
$$a_{PL,DP}^N TI = [10^{-4}, 10^{-2}]$$
$$a_{DP,PL}^0 = [-10^{-5}, -10^{-7}]$$
$$a_{DP,PL}^N TI = [-10^{-2}, -10^{-4}]$$

The N_0 parameters in previous equations represent a typical average abundance of the non-trophic interactor. These values were taken, when possible, from

Pérez-Mellado et al. (2000, 2006). Diptera densities were approximated based on Braack and Retief (1986):

$$N_{PL}^0 = 2189$$
$$N_{DP}^0 = 150$$
$$N_{SV}^0 = 3000$$
$$N_{HM}^0 = 7187$$
$$N_{PLe}^0 = 187$$
$$N_{CM}^0 = 10000$$

Equal Footing Network

The model is of the form:

$$\frac{dN_x}{dt} = r_x N_x \tag{7.9}$$

where

$$r_x = r_x^0 + \sum_{y \in S, y \neq x} a_{xy} N_y - \left(\beta_x + c_x \sum_{y \in S, y \neq x} a_{xy} N_y \right) N_x \tag{7.10}$$

As with the Expanded Food Web model, we constrained each free parameter to a given range and simulated 100000 times the system for 2500 time steps, assigning a random value to each parameter within its range. Here we varied the strength of the antagonistic and facilitative interactions (commensalistic and mutualistic) and checked the stability of the resulting network by means of a local stability analysis.

$$r_{FT} = [-0.01, -0.001]$$
$$r_{PL} = [0.01, 0.1]$$
$$r_{DP} = [0.4, 0.6]$$
$$r_{SV} = [0.05, 0.15]$$
$$r_{HM} = [0.15, 0.25]$$
$$r_{PLe} = [0.05, 0.15]$$
$$r_{CM} = [0.15, 0.25]$$
$$\beta_x = [10^{-5}, 10^{-4}] \forall x$$
$$c_x = 10^{-3} \forall x$$

Interaction strengths

1. Weak interactions

$$a_{FT,PL} = [10^{-7}, 10^{-5}]$$
$$a_{PL,FT} = [-10^{-5}, -10^{-7}]$$
$$a_{PL,DP} = [10^{-7}, 10^{-5}]$$
$$a_{PL,HM} = [10^{-7}, 10^{-5}]$$
$$a_{PL,PLe} = [10^{-7}, 10^{-5}]$$
$$a_{PL,CM} = [10^{-7}, 10^{-5}]$$
$$a_{DP,PL} = [-10^{-5}, -10^{-7}]$$
$$a_{DP,HM} = [10^{-7}, 10^{-5}]$$
$$a_{HM,PL} = [10^{-7}, 10^{-5}]$$
$$a_{HM,DP} = [10^{-7}, 10^{-5}]$$
$$a_{PLe,PL} = [10^{-7}, -10^{-5}]$$
$$a_{CM,PL} = [10^{-7}, -10^{-5}]$$

2. Strong antagonisms

$$a_{FT,PL} = [10^{-4}, 10^{-2}]$$
$$a_{PL,FT} = [-10^{-2}, -10^{-4}]$$
$$a_{PL,DP} = [10^{-4}, 10^{-2}]$$
$$a_{PL,HM} = [10^{-7}, 10^{-5}]$$
$$a_{PL,PLe} = [10^{-7}, 10^{-5}]$$
$$a_{PL,CM} = [10^{-7}, 10^{-5}]$$
$$a_{DP,PL} = [-10^{-2}, -10^{-4}]$$
$$a_{DP,HM} = [10^{-7}, 10^{-5}]$$
$$a_{HM,PL} = [10^{-7}, 10^{-5}]$$
$$a_{HM,DP} = [10^{-7}, 10^{-5}]$$
$$a_{PLe,PL} = [10^{-7}, -10^{-5}]$$
$$a_{CM,PL} = [10^{-7}, -10^{-5}]$$

3. Strong facilitation

$$a_{FT,PL} = [10^{-7}, 10^{-5}]$$
$$a_{PL,FT} = [-10^{-5}, -10^{-7}]$$
$$a_{PL,DP} = [10^{-7}, 10^{-5}]$$
$$a_{PL,HM} = [10^{-4}, 10^{-2}]$$
$$a_{PL,PLe} = [10^{-4}, 10^{-2}]$$
$$a_{PL,CM} = [10^{-4}, 10^{-2}]$$
$$a_{DP,PL} = [-10^{-5}, -10^{-7}]$$
$$a_{DP,HM} = [10^{-4}, 10^{-2}]$$
$$a_{HM,PL} = [10^{-4}, 10^{-2}]$$
$$a_{HM,DP} = [10^{-4}, 10^{-2}]$$
$$a_{PLe,PL} = [10^{-4}, -10^{-2}]$$
$$a_{CM,PL} = [10^{-4}, -10^{-2}]$$

Appendix 2.2: Chapter 2 - Adjacency matrices and multilayer representations

Networks with static interaction strength coefficients can be represented consistently through adjacency matrices. Here we show, for the three frameworks presented, the adjacency matrices representing the Aire Island community. We also discuss alternative representations of ecological networks in the multilayer framework.

Expanded Food Webs

In the formulation used, we modelled four ecological mechanisms: trophic interactions, nontrophic interactions that affect growth rate, and nontrophic interactions that affect mortality rate, as well as interaction modifiers. The three first mechanisms are represented by one adjacency matrix. Interaction modifiers represent the effect of one species on a given interaction, so that in a community of N species, N potential interaction modifiers matrices could exist. In the matrices (Fig. A.2.2.1) we adhere to the definitions adopted in Chapter 2, in that we consider the feeding element of mutualisms as trophic interactions, while the subsequent benefits for the plant species are considered as non-trophic interactions.
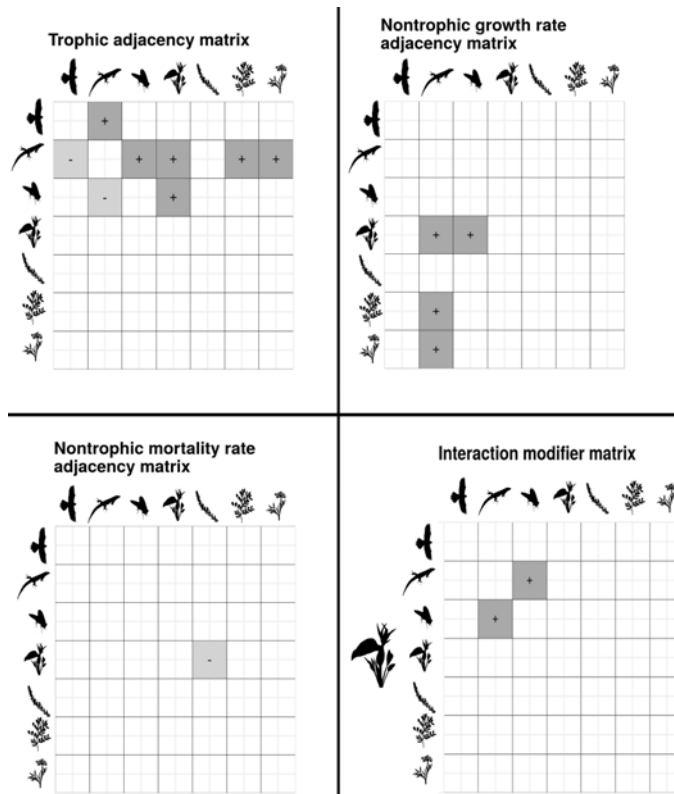
Figure A.2.2.1: Adjacency matrices of the Expanded food web of the Aire Island community. In the trophic adjacency matrix, signs indicate effects of species in columns over species in rows. In the nontrophic matrices, signs indicate the effect of species in columns over the growth and mortality rates of the species in rows, respectively. In the interaction modifier matrix, the whole matrix represents the effects of Helicodiceros muscivorus (leftmost silhouette) over the community trophic interactions. The positive signs indicate that the presence of the dead horse arum increases the absolute magnitude of the Podarcis lilfordi – Diptera interaction. As this is the only interaction modifier considered in the community, the other six interaction modifier matrices are not shown.

Multilayer Networks

Representing multiple interaction types with multilayer networks

Due to the flexibility of the multilayer framework, it is often possible to design representations of the same network with different layering dimensions (see section 2.4 of Kivelä et al. (2014), where they frame the discussion in terms of node-coloured and edge-coloured graphs). In the context of ecological networks with different interaction types, different layers usually represent different interaction types, but another option is to separate layers by taxonomic groups, so that intra-layer links represent these within a given guild and inter-layer links are between-guild interactions (Fig. A.2.2.2, cf. Fig. 2.3). In the first representation, emphasis is given to the sub-networks of different interaction types, and their structure and dynamics can be tracked separatedly. In the second one, the guild structure of the community is the priority, and it is a natural representation for analyzing patterns of interactions of the different guilds or differences in within-

guild and between-guild interactions. In terms of network structure, the first representation is potentially node-aligned, i.e. all nodes can appear in all layers, and there is at least one intra-layer link for each layer. The second representation, however, is layer-disjoint, i.e. a node exists at most in one layer, and there can exist layers without any intra-layer links. In that sense, thus, the guild representation does not connect subnetworks, but sets of entities. We have found no explicit examples of the guild representation in ecological studies, but empirical datasets such as the one compiled by (Pocock et al., 2012) can be looked at in both ways of representation.
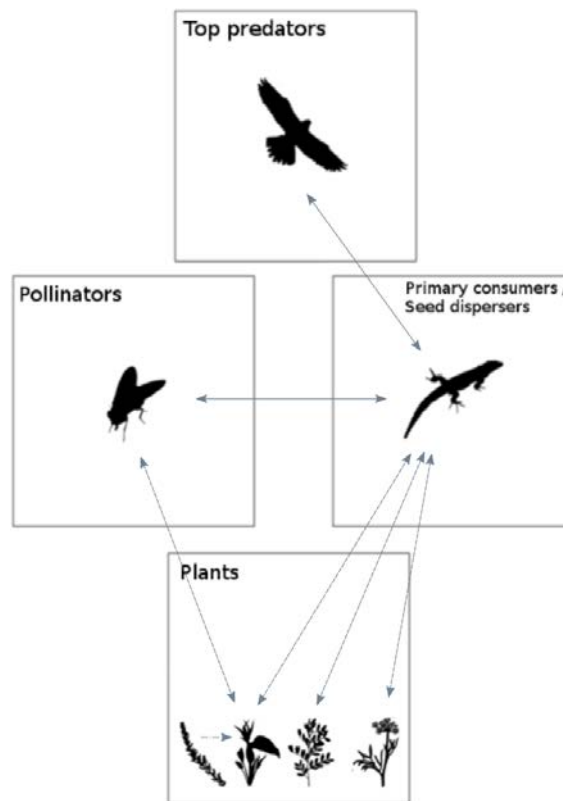
FIGURE A.2.2.2: A multilayer representation of the Aire Island community where layers represent functional guilds. Note how in this representation, only one intra-layer link exists, that of the commensalist relationship between *Suaeda vera* and *Helicodiceros muscivorus*. In each interaction, an arrow tip indicates a non-neutral effect over a species.

Adjacency matrices of multiplex networks

Multilayer networks can be represented consistently as $rank - 2(d + 1)$ adjacency tensors, where d is the number of aspects or dimensions of the network (Kivelä et al., 2014). The tensorial representation is only valid for node-aligned networks, i.e. networks in which all nodes are represented in all layers. While this constraint can be relaxed (see Kivelä et al. 2014 for details), multilayer networks can also be represented through so-called supra-adjacency matrices, whereby one loses some information about the aspects (due to the "flattening" of the network) but one can represent networks that are not node-aligned and, importantly, use standard

matrix algebra to analyze network structure. These supra-adjacency matrices represent in the same structure the three types of links potentially present in multilayer networks: intra-layer links in the diagonal blocks, coupling links in the diagonal elements of the off-diagonal blocks, and inter-layer links in the off-diagonal elements of the off-diagonal blocks (Fig. A.2.2.3). The distinction between coupling and inter-layer links is that coupling links are connecting the same node in different layers, while inter-layer links connect different nodes in different layers. The Aire Island multilayer network, where each layer is an interaction type, is not node-aligned (i.e. not all nodes are present in all layers), hence the supra-adjacency matrix is not square and not all coupling links are realized (Fig. A.2.2.4).
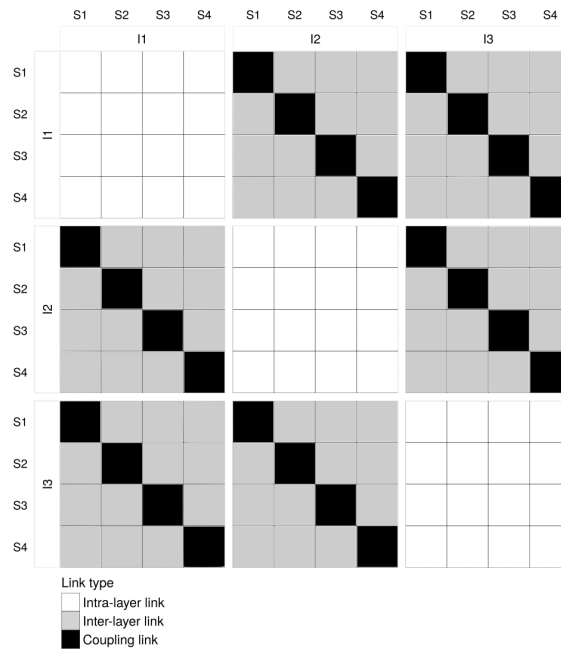
Figure A.2.2.3: An example of supra-adjacency matrix showing the placement of intra-layer, coupling and inter-layer links. In this setting, the network consists of four nodes (S1-S4) interacting in three different ways (I1-I3). All four species are represented in the three sub-networks, so that the network is node-aligned. Blocks are slightly separated for visibility
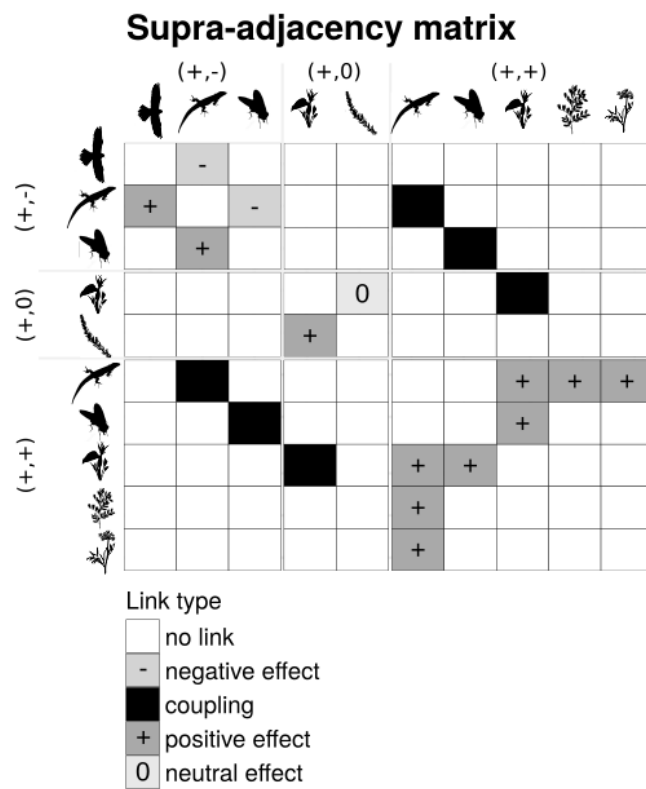
Figure A.2.2.4: Supra-adjacency matrix of the Aire Island multilayer network. The (+,-) block represents the antagonist subnetwork, (+,0) the commensalist one and (+,+) the mutualist one.

Appendix 2.3: Chapter 2 - Supplementary results
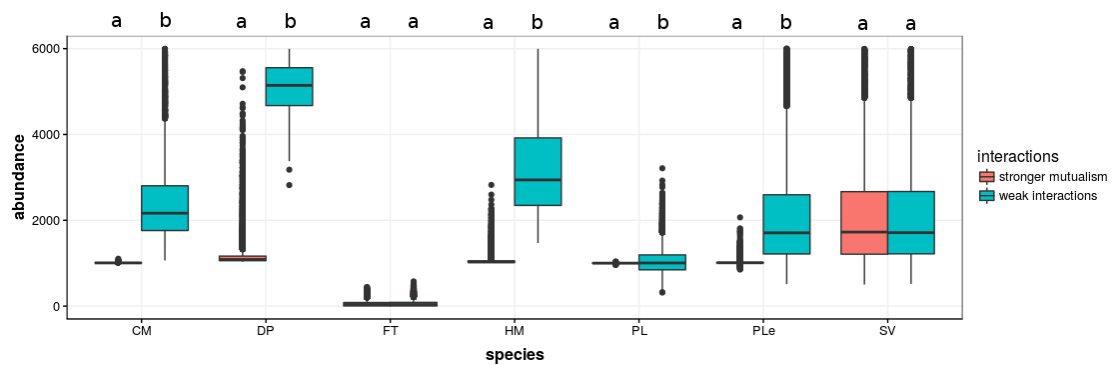
FigURE A.2.3.1: Equilibrium abundances of the Aire Island community obtained with the equal footing approach (cf. Fig. 2.3). Each box represents the distribution of abundances for each species from the 19991 simulations with leading eigenvalue ¡ 0. Simulations with strong antagonistic interactions are not shown since a vast majority of them were unstable. Letters above boxplots indicate significant differences according to Wilcoxon signed-rank tests (CM: W = 19, p ¡ 0.05; DP: W = 12405, p ¡ 0.05; FT: W = 50107000, p = 0.794; HM: W = 58732, p ¡ 0.05; PL: W = 49102000, p ¡ 0.05; PLe: W = 14983000, p ¡ 0.05; SV: W = 49815000, p = 0.649)
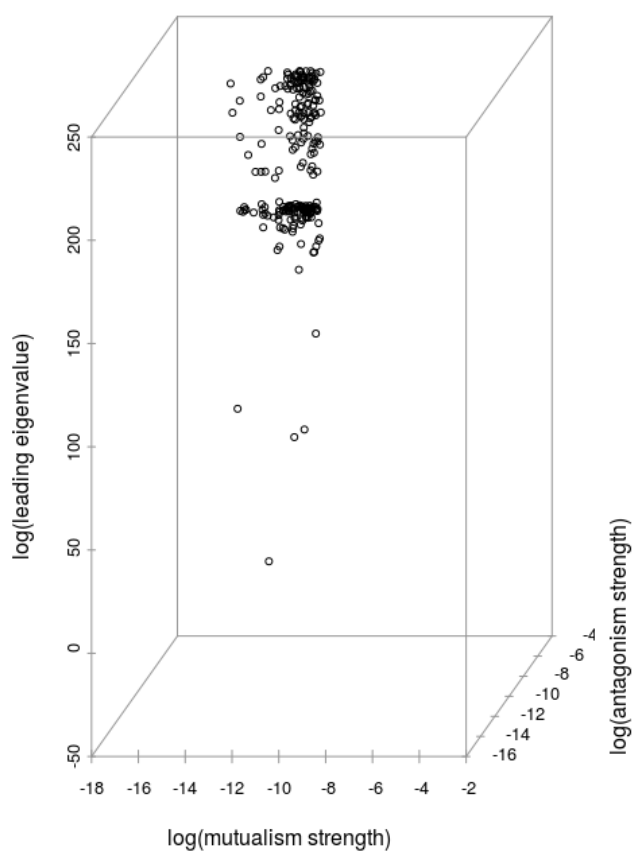
Figure A.2.3.2: Distribution of the leading eigenvalues of unstable communities modelled with the equal footing approach and not shown in Fig. 2.4. In that figure only leading eigenvalues close to 0 where shown for visibility, here, all remaining values have been log-scaled.

Appendix 3.1: Chapter 3 - Model parameterization and implementation

Model parameterization

The parameters of the model from Chapter 3 refer to properties of 1) the whole community, 2) the strength of each interaction type, or 3) species performance. In the tables, the following abbreviations are used: AM = amensalism, AN = antagonism, CM = commensalism, CP = competition, M = mutualism.

Table A.3.1.1: Community-level parameters.

Initial number of species	{20, 40, 60}
Initial Interaction Type Ratio	{{AM = 0.2, AN = 0.2, CM = 0.2, CP = 0.2, M = 0.2}, {AM = 0.4, AN = 0.15, CM = 0.15, CP = O.15, M = 0.15}, {AM = 0.15, AN = 0.4, CM = 0.15, CP = O.15, M = 0.15}, {AM = 0.15, AN = 0.15, CM = 0.4, CP = O.15, M = 0.15}, {AM = 0.15, AN = 0.15, CM = 0.15, CP = O.4, M = 0.15}, {AM = 0.15, AN = 0.15, CM = 0.15, CP = O.15, M = 0.4}}
Overall connectance	0.5
Initial SAD	Gambin
Initial SAD parameters	$\alpha = 2$
Number of discrete trophic levels	4
Trophic level abundance scaling exponent	0.75
Abundance of basal trophic level	100 * initial number of species

Table A.3.1.2: Probabilities of occurrence of each interaction type (Fig. 3.1 of chapter 3). The complete list of studies included can be found at the online supplementary material of the published article: https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2465

Interaction	Trophic levels	Prob
Amensalism	same	1
Amensalism	adjacent	0
Amensalism	other	0
Antagonism	same	0.015
Antagonism	adjacent	0.918
Antagonism	other	0.067
Commensalism	same	0.661
Commensalism	adjacent	0.292
Commensalism	other	0.047
Competition	same	0.979
Competition	adjacent	0.021
Competition	other	0
Mutualism	same	0.048
Mutualism	adjacent	0.854
Mutualism	other	0.098

The range of k parameters was chosen so that antagonistic interactions had a greater effect than other types, as they usually result in the death of the prey. In the same vein, the a parameter is an order of magnitude smaller for antagonistic interactions due to assumed defense mechanisms by resource species. The x_0 parameter does not have a specific ecological meaning in the context of our study, so we chose to keep it constant.

Table A.3.1.3: Interaction-level parameters.

k	{AM = 0.1, AN = 0.5, CM = 0.1, CP = 0.1, M = 0.1}
a	{AM = 0.01, AN = 0.001, CM = 0.01, CP = 0.01, M = 0.01}
x_0	1

Basal species were assumed to have positive intrinsic growth rates, as opposed to species in higher trophic levels. Other parameters were in the range used by García-Algarra et al. (2014), the initial formulation of Eq. (3.5) in Chapter 3.

Table A.3.1.4: Species-level parameters.

r	basal species: (0,0.08)
	consumers: (-0.08,0)
c	0.001
α	$(1 * 10^{-5}, 1 * 10^{-4})$

Model implementation

The model is developed in R 3.0 (R Core Team, 2018), and makes use, mainly, of the package deSolve (Soetaert et al., 2012) and the package suite tidyverse (www.tidyverse.org) for generation and treatment of results. Here we show how communities are assembled in terms of 1) their distribution of abundances and trophic levels, and 2) their interaction networks. In the last section, we expand on how model parameters are selected for solving the dynamical system.
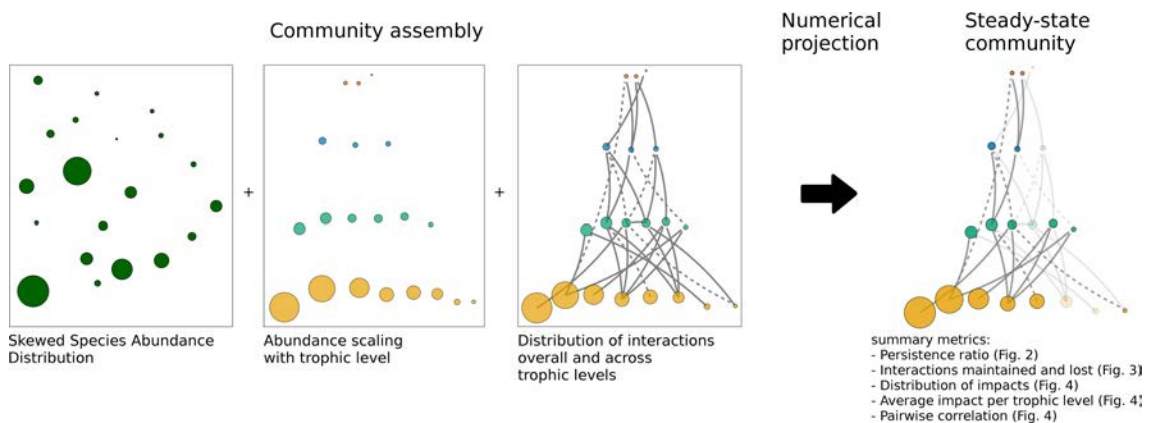
Figure A.3.1.1: Conceptual diagram of the model, showing 20 model species and two interaction types (solid and dashed lines). Abundances are proportional to the size of the node. The process depicted is replicated 1000 times for each configuration of species richness and frequency of interaction types.

Community assembly process

1. Abundance and trophic level structure

The initial abundances of species and its (discrete) trophic level (first and second box of Fig. A.3.1.1) are calculated by a function named `AssignTrophicLevel`. This function is able generate communities of any number of species and discrete trophic levels, with different initial SADs, and with or without abundance scaling with trophic level. We will show the workflow of this function by "building" a community with the following parameters, similar to the model communities

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analyzed in chapter 3:

```r
# number of species
num.sp <- 40
# number of discrete trophic levels
trophic.levels <- 4
# SAD parameters
abundance.distribution <- "gambin"
gambin.alpha <- 2
gambin.maxoctave <- 8
# include abundance scaling with trophic level
scaling.law.tl <- TRUE
# with exponent 3/4
scaling.exponent.tl <- 0.75
# aggregated abundance of the basal trophic level, necessary for the scaling
basal.abundance <- num.sp * 100
```

The first task is to calculate the aggregated abundances of each trophic level, according to the scaling. We added a small white noise term $\epsilon \sim N(0, abundance/10)$ to introduce an element of small variability:

```r
trophic.level.abundance <- numeric(trophic.levels)
trophic.level.abundance[1] <- basal.abundance

# calculate abundance for each trophic level
# including a white noise term with mean = 0 and sd = abundance/10
if(length(trophic.level.abundance) > 1){
  for(i.trophic.level in 2:trophic.levels){
    trophic.level.abundance[i.trophic.level] <-
      trophic.level.abundance[i.trophic.level - 1]^scaling.exponent.tl
    trophic.level.abundance[i.trophic.level] <-
      trophic.level.abundance[i.trophic.level] +
      rnorm(n = 1,mean = 0,sd = trophic.level.abundance[i.trophic.level]/10)
  }
}
```

This gives the following abundances (rounded to integer) for the four trophic levels defined:

```
[1] 4000   489   112    34
```

Next, the abundance of each species is drawn from the distribution specified, in this case, a discrete gambin with $\alpha = 2$. We developed a function GenerateProb-Numbers to incorporate this functionality in our model. Further details on how the function deals with the transformation from octaves to actual abundances can be checked in the documentation and code of the function.

```
abundance.list <- DGC::GenerateProbNumbers(times = num.sp,
                                           dist = abundance.distribution,
                                           cum.sum = sum(trophic.level.abundance),
                                           gambin.alpha = gambin.alpha,
                                           gambin.maxoctave = gambin.maxoctave)
```

returns the following abundance distribution:
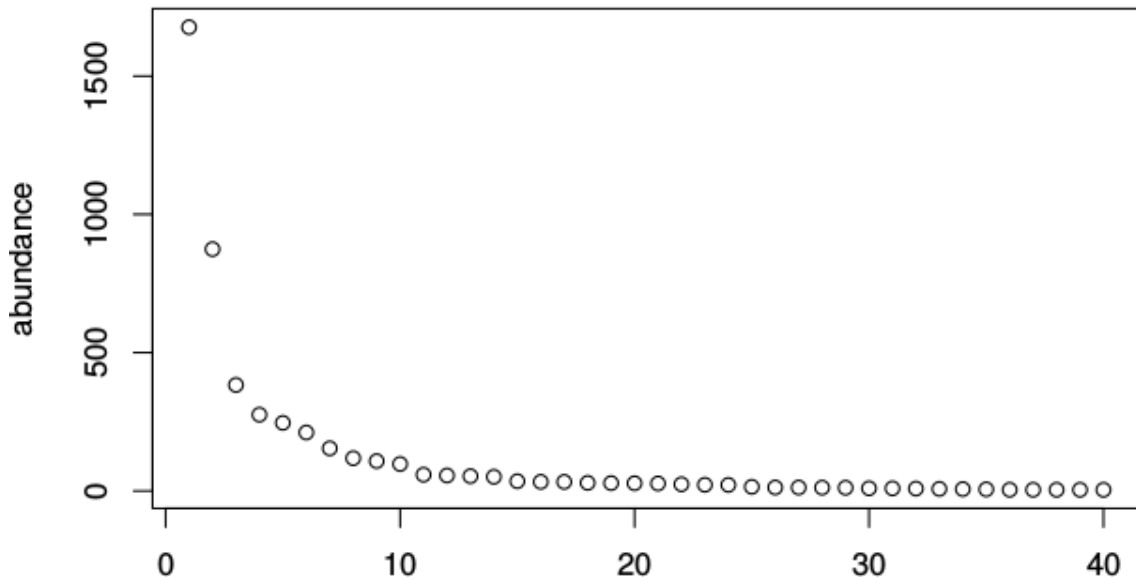
FIGURE A.3.1.2: Abundance distribution for a community of 40 species generated with the parameterization of the main simulations.

At this stage, species have initial abundances but are not assigned to trophic levels. The next piece of R code assigns species to trophic levels ensuring that the aggregated abundances of a trophic level are consisten with the scaling already calculated. Again, a certain tolerance is allowed, so that abundances will not need to exactly follow the expected scaling.

```
# create the dataframe
tl.results <- data.frame(species = c(1:length(abundance.list)),
                         abundance = sort(abundance.list,decreasing = T),
                         trophic.level = 0)

# the most abundant species will always be at the basal level
tl.results$trophic.level[1] <- 1

for(i.tl in trophic.levels:1){

  # iterative process: add species until a trophic level is "filled".
  # For convenience I start in the upper trophic level,
  # since it will be the most difficult to fill
```

```r
  # (few species will have such low abundances)

  if(i.tl == 1){
    my.abund <- tl.results$abundance[1]
  }else{
    my.abund <- 0
  }

  # certain tolerance, it does not need to be exact
  tl.tolerance <- trophic.level.abundance[i.tl]*0.1

  my.sp <- 0

  # while the abundance of the i.tl trophic level is not within the tolerance levels,
  # keep adding species
  while(length(my.sp) != 0 &
        findInterval(my.abund,c(trophic.level.abundance[i.tl] - tl.tolerance,
                                trophic.level.abundance[i.tl] + tl.tolerance)) != 1){

    # potential species
    my.sp <- which(tl.results$trophic.level == 0 &
                     tl.results$abundance + my.abund <
                     (trophic.level.abundance[i.tl] + tl.tolerance))

    # sample from the potential species pool
    if(length(my.sp)>0){
      my.sp <- ifelse(length(my.sp) == 1,my.sp,sample(my.sp,size = 1))
      my.abund <- my.abund + tl.results$abundance[tl.results$species == my.sp]
      tl.results$trophic.level[tl.results$species == my.sp] <- i.tl
    }# if
  }# while

}# for i.tl

# if any species remains unassigned, randomly assign it to the 1st or 2nd trophic levels
if(sum(tl.results$trophic.level == 0) > 0){
  tl.results$trophic.level[tl.results$trophic.level == 0] <-
    sample(1:2,size = sum(tl.results$trophic.level == 0),replace = T)
}
```

The obtained model community looks like this:

```
    species    abundance trophic.level
1         1 1676.620271             1
2         2  874.111429             1
3         3  383.063086             1
4         4  275.592134             1
5         5  246.110064             1
6         6  211.205096             1
```

7	7	153.851103	2
8	8	118.274729	1
9	9	107.833539	2
10	10	97.232796	2
11	11	58.662382	1
12	12	55.807177	2
13	13	53.431286	2
14	14	50.988303	2
15	15	35.071829	2
16	16	32.799469	3
17	17	32.632668	1
18	18	29.118406	2
19	19	28.265496	1
20	20	27.696220	2
21	21	26.767967	3
22	22	23.981084	2
23	23	22.095900	3
24	24	21.646918	1
25	25	14.770477	2
26	26	12.470659	2
27	27	12.385128	3
28	28	11.899331	2
29	29	11.529057	2
30	30	9.390576	2
31	31	9.270894	4
32	32	8.353354	4
33	33	7.347363	4
34	34	6.604980	4
35	35	5.828236	3
36	36	4.154809	1
37	37	4.148890	4
38	38	4.046894	2
39	39	4.019357	2
40	40	3.991716	3

2. Building the network of interactions

The sign matrix of the community, as used in this study, is a square matrix containing the sign of the effects of every species upon every other species of the community. These signs can be either -1, 0, or 1. For constructing such a matrix, we need different information: first, the list of species and their trophic levels; second, the connectance of the network; third, the frequencies of the five interaction types; fourth, the probabilities for each interaction type to occur in same, adjacent or other trophic levels. This information is passed to the function `GenerateSignMatrix`. In this example, we use the species list calculated above, and specify an equal ratio of interaction types, alongside a connectance of 0.5. Furthermore, we use the probabilities of interaction ocurrence across trophic levels shown in Fig. 3.1 of chapter 3.

Due to the cumbersomeness of the `GenerateSignMatrix` function, here we

summarize its general idea, and leave the reader the option to consult the complete function in the Github repository of David García Callejas (`http://github.com/DavidGarciaCallejas/DGC`). First, the function obtains the maximum number of links that can potentially be assigned to each interaction type (bear in mind that some combinations of links across trophic levels may have zero probability of occurring, e.g. amensalism between adjacent or other trophic levels. Therefore, the set of potential amensalistic links is much more reduced than the set of, say, potential mutualistic links. Appendix 2.4 delves further into this idea and its implications). Second, the function obtains the overall number of links to be actually assigned, based on network connectance. Lastly, it instantiates each of these links by 1) drawing an interaction type according to the probabilities specified, in this case (0.2, 0.2, 0.2, 0.2, 0.2); 2) drawing the trophic levels involved according to the probabilities of occurrence across trophic levels (Fig. 3.1 of chapter 3); 3) randomly selecting one of the potential links with these characteristics not yet "filled". Note that, as the process of selecting links is stochastic, the realized frequencies of interaction types will not equal the expected ones, and the same will happen with the probabilities of occurrence across trophic levels. With the above parameters, a realization of a sign matrix may present the following summarized information:

- Number of interactions of each of the five interaction types:

```
   competition      amensalism      antagonism      mutualism    commensalism
           80              70              90             69              81
no.interaction
          390
```

- Realized frequency of each of the five interaction types:

```
[1] 0.2051282 0.1794872 0.2307692 0.1769231 0.2076923
```

- Realized overall network connectance:

```
[1] 0.5
```

- Connectance of every interaction type relative to its set of available links:

```
 competition      amensalism      antagonism      mutualism  commensalism
  0.14209591      0.30837004      0.11538462      0.08846154    0.10384615
```

- Realized ratios of interaction occurrence across trophic levels (cf. Table A.3.1.2):

```
# A tibble: 10 x 4
# Groups:    type [5]
     type        trophic.level      n relative.frequency
     <chr>       <chr>          <int>              <dbl>
 1 amensalism   same              70             1.00
 2 antagonism   adjacent         168             0.933
 3 antagonism   other              8             0.0440
 4 antagonism   same               4             0.0220
 5 commensalism adjacent          24             0.296
 6 commensalism other              3             0.0370
 7 commensalism same              54             0.667
 8 competition  same             160             1.00
 9 mutualism    adjacent         128             0.928
10 mutualism    other             10             0.0720
```

Parameter selection and system solving

Community-level parameters and interaction parameters are fixed in the model
(Tables A.3.1.1, A.3.1.2, A.3.1.3) but the realized interaction matrix is different in
each realization. Species-level parameters r_0 and α are specified as an interval of
potential values (Table A.3.1.4), and each realization draws a random value for
each species from these intervals.

```
### min and max parameter values
min.r0 <- -0.08
max.r0 <- 0.08
min.c0 <- 0.001
max.c0 <- 0.001
min.alpha <- 1e-05
max.alpha <- 1e-04
# extinction threshold
extinction.threshold <- 0.001
# scale factor: competition, amensalism, antagonism, mutualism, commensalism
scale.factor <- c(0.1, 0.1, 0.5, 0.1, 0.1)
# parameter 'a' of the IF function competition, amensalism, antagonism,
# mutualism, commensalism
IF.success.rate <- c(0.01, 0.01, 0.001, 0.01, 0.01)
# extra parameter of the logistic
x0 <- 1

# create list of parameters for the dynamic equations model
param.list <- list()

# if trophic.level > 1, r<0
param.list$r0 <- sapply(tl.results$trophic.level, FUN = function(x) ifelse(x >
    1, runif(1, min.r0, 0), runif(1, 0, max.r0)))
```

```
param.list$c0 <- runif(num.sp, min.c0, max.c0)
param.list$alpha <- runif(num.sp, min.alpha, max.alpha)
param.list$sign.matrix <- sign.matrix
param.list$interaction.types <- InteractionTypes(sign.matrix)
param.list$scale.factor <- scale.factor
param.list$IF.success <- IF.success.rate
param.list$x0 <- x0
param.list$extinction.threshold <- extinction.threshold
```

The system is solved numerically with a Range-Kutta approximation, using the deSolve package.

```
dynamics <- ode(y = tl.results$abundance, times = time.steps, func = network.model,
    parms = param.list, method = "rk4")
```
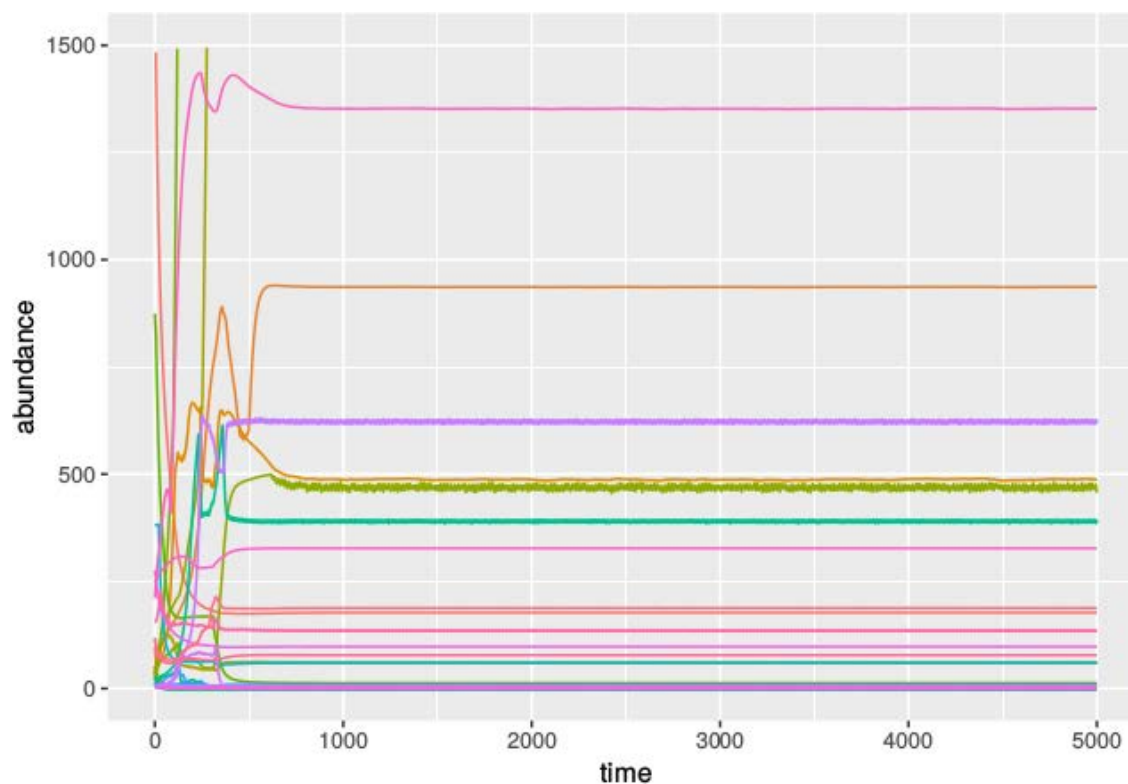

Figure A.3.1.3: Dynamics of the abundances of a 40-species community, up to 5000 timesteps.

Appendix 3.2: Chapter 3 - Supplementary results

Here we present the results of the statistical tests associated with Fig. 3.2, Fig. 3.3, and Fig. 3.4 of Chapter 3. In addition, we show how persistence values, i.e. Fig. 3.2 of Chapter 3, vary across trophic levels (Fig. A.3.2.1), and how average species impact vary with increasing species richness A.3.2.1). In the following tables, the following abbreviations are used referring to simulations with varying interaction frequencies: ER = Equal ratio among interaction types, HAM = High amensalism, HAN = High antagonism, HCM = High commensalism, HCP = High competition, HM = High mutualism.

1. Differences between persistence levels across simulations (Fig. Fig. 3.2 of Chapter 3)

We tested whether the distributions of persistence values for each category of interaction frequency were different or not. For that, we grouped the observations according to the initial richness of the simulations and, for each level of initial richness, we performed a Kruskal-Wallis rank test for differences in the distributions of persistence across the six levels of interaction frequencies (Table A.3.2.1). Kruskal-Wallis test are non-parametric tests appropriate for testing whether sets of samples originate from the same distribution. These tests showed significant differences between persistence distributions within each richness level, so we performed post-hoc Dunn tests for the difference between every pair of distributions, again within each richness level (Table A.3.2.2). P-values were adjusted with the Bonferroni correction. All pairs of distributions were significantly different except that of the "equal ratio" and "high antagonism" simulations with 40 initial species.

Table A.3.2.1: Kruskal-Wallis rank tests for differences between pairs of persistence distributions.

Initial richness	χ^2	Df	p-value
20	1430.6	5	< 0.001
40	1349.6	5	< 0.001
60	552.69	5	< 0.001

Table A.3.2.2: Pair-wise post-hoc Dunn's test comparisons for every pair of simulations.

Pair	Initial richness	Z statistic	p-value
ER - HAM	20	7.657	< 0.001
ER - HAM	40	8.388	< 0.001
ER - HAM	60	8.589	< 0.001
ER - HAN	20	3.909	< 0.001
ER - HAN	40	0.559	1
ER - HAN	60	4.019	< 0.001
ER - HCM	20	-7.388	< 0.001
ER - HCM	40	-8.674	< 0.001
ER - HCM	60	-3.971	< 0.001
ER - HCP	20	13.56	< 0.001
ER - HCP	40	12.89	< 0.001
ER - HCP	60	12.04	< 0.001
ER - HM	20	-20.09	< 0.001
ER - HM	40	-19.21	< 0.001
ER - HM	60	-7.414	< 0.001
HAM - HAN	20	-3.749	0.0013
HAM - HAN	40	-7.829	< 0.001
HAM - HAN	60	-4.569	< 0.001
HAM - HCM	20	-15.045	< 0.001
HAM - HCM	40	-17.062	< 0.001
HAM - HCM	60	-12.56	< 0.001
HAM - HCP	20	5.903	< 0.001
HAM - HCP	40	4.497	< 0.001
HAM - HCP	60	3.452	0.0042
HAM - HM	20	-27.75	< 0.001
HAM - HM	40	-27.59	< 0.001
HAM - HM	60	-16.004	< 0.001
HAN - HCM	20	-11.297	< 0.001
HAN - HCM	40	-9.233	< 0.001
HAN - HCM	60	-7.991	< 0.001
HAN - HCP	20	9.651	< 0.001
HAN - HCP	40	12.33	< 0.001
HAN - HCP	60	8.021	< 0.001
HAN - HM	20	-24.01	< 0.001
HAN - HM	40	-19.77	< 0.001
HAN - HM	60	-11.43	< 0.001
HCM - HCP	20	20.95	< 0.001
HCM - HCP	40	24.56	< 0.001
HCM - HCP	60	16.01	< 0.001
HCM - HM	20	-12.71	< 0.001
HCM - HM	40	-10.53	< 0.001
HCM - HM	60	-3.44	0.0043
HCP - HM	20	-33.66	< 0.001

Pair	Initial richness	Z statistic	p-value
HCP - HM	40	-32.09	< 0.001
HCP - HM	60	-19.46	< 0.001

2. Differences between the initial and final frequencies of interaction (Fig. 3.3 of Chapter 3)

For testing the difference between the initial and final frequency of each interaction type, we performed Wilcoxon paired signed-rank tests for each combination of initial richness and level of interaction frequency. These tests allow a non-parametric analysis of the difference between paired samples. In our case, each paired sample was the initial and final frequency of a given interaction type. In particular, for each replicate of each simulation, we calculated whether the mean rank of the initial-final differences was either less, different or greater than zero. These alternative hypotheses were selected based on a preliminary inspection of the data.

Table A.3.2.3: Wilcoxon paired signed-rank tests for testing differences between the initial and final frequency of each interaction type (Fig. 3.3). The interaction type column refers to the set of interactions analysed. For example, "amensalism" refers to the ratio of amensalistic interactions in all simulations, e.g. the whole set of points from the upper-left panel, while "amensalism - HAM" refers to the set of amensalistic interactions in the simulation with high initial amensalism, e.g. the set of blue points in the upper-left panel. The p-values listed here correspond to the graphical legend of Fig. 3.3.

Initial richness	Interaction type	alternative hypothesis	Statistic	P-value
20	amensalism	initial > final	10268730	< 0.001
20	antagonism	initial > final	11714319	< 0.001
20	commensalism	initial < final	6224456	< 0.001
20	competition	initial > final	12883361	< 0.001
20	mutualism	initial < final	2776289	< 0.001
20	amensalism - HAM	initial > final	270371	< 0.01
20	antagonism - HAN	initial > final	325119	< 0.001
20	commensalism - HCM	initial < final	111677	< 0.001
20	competition - HCP	initial > final	369222	< 0.001
20	mutualism - HM	initial < final	14319	< 0.001
40	amensalism	initial > final	12107905	< 0.001
40	antagonism	initial != final	9150881	0.084
40	commensalism	initial < final	7655927	< 0.001
40	competition	initial > final	13361816	< 0.001
40	mutualism	initial < final	2669916	< 0.001
40	amensalism - HAM	initial > final	288792	< 0.001
40	antagonism - HAN	initial != final	238615	0.249
40	commensalism - HCM	initial < final	178367	< 0.001

Initial richness	Interaction type	alternative hypothesis	Statistic	P-value
40	competition - HCP	initial > final	274399	< 0.01
40	mutualism - HM	initial < final	2259	< 0.001
60	amensalism	initial > final	16351320	< 0.001
60	antagonism	initial < final	2340004	< 0.001
60	commensalism	initial > final	11596381	< 0.001
60	competition	initial > final	16700652	< 0.001
60	mutualism	initial < final	579985	< 0.001
60	amensalism - HAM	initial > final	449342	< 0.01
60	antagonism - HAN	initial < final	33262	< 0.001
60	commensalism - HCM	initial > final	352325	< 0.001
60	competition - HCP	initial > final	412015	< 0.001
60	mutualism - HM	initial < final	137	< 0.001

3. Structural patterns of the model communities (Fig. 3.4 of Chapter 3)

We checked the skewness of the distribution of species impacts by calculating the Pearson's moment coefficient of skewness for every simulation (Table A.3.2.4). Furthermore, we analyzed the differences between distributions of species impact per trophic level. For that, we performed a Kruskal-Wallis test followed by post-hoc Dunn tests, in a similar vein to the tests of section **1**. In this case, all pairs of species impacts distributions were significantly different.

Table A.3.2.4: Pearson's moment coefficient of skewness of the distribution of net species impacts per simulation type (in panel a of Fig. 3.4 of Chapter 3, the simulation with 60 species and equal ratio between interactions is depicted

Initial richness	Frequency of interaction types	Skewness
20	Equal ratio	12.6
20	High amensalism	22.1
20	High antagonism	18.7
20	High commensalism	7.7
20	High competition	24.1
20	High mutualism	8.9
40	Equal ratio	11.2
40	High amensalism	20.2
40	High antagonism	20.2
40	High commensalism	8.9
40	High competition	19.8
40	High mutualism	11.5
60	Equal ratio	14.7
60	High amensalism	20.3
60	High antagonism	15.0
60	High commensalism	10.3
60	High competition	18.3

Initial richness	Frequency of interaction types	Skewness
60	High mutualism	15.0

Table A.3.2.5: Kruskal-Wallis rank tests for two-tail differences between average impact per trophic level (in panel b of Fig. 3.4 of Chapter 3, the simulation with 60 species and equal ratio between interactions is depicted)

Initial richness	Frequency of interaction type	s χ^2	Df	p-value
20	Equal ratio	43360.4	3	< 0.001
20	High amensalism	38160.2	3	< 0.001
20	High antagonism	51881.4	3	< 0.001
20	High commensalism	43279.1	3	< 0.001
20	High competition	42625.5	3	< 0.001
20	High mutualism	48095.8	3	< 0.001
40	Equal ratio	65136.7	3	< 0.001
40	High amensalism	57615.3	3	< 0.001
40	High antagonism	112336.0	3	< 0.001
40	High commensalism	66019.0	3	< 0.001
40	High competition	57758.8	3	< 0.001
40	High mutualism	71763.3	3	< 0.001
60	Equal ratio	99168.1	3	< 0.001
60	High amensalism	73536.4	3	< 0.001
60	High antagonism	210780.8	3	< 0.001
60	High commensalism	81705.7	3	< 0.001
60	High competition	83325.2	3	< 0.001
60	High mutualism	92851.8	3	< 0.001

Table A.3.2.6: Pair-wise post-hoc Dunn's test comparisons of the results of table A.3.2.5, for difference in average impact per trophic level. For each combination of initial richness and interaction frequencies, average impact values of every pair of trophic levels are compared

Initial richness	Frequency of interaction types	Trophic level pair	Z statistic	p-value
20	Equal ratio	1-2	113.5	< 0.001
20	Equal ratio	1-3	155.5	< 0.001
20	Equal ratio	1-4	145.4	< 0.001
20	Equal ratio	2-3	76.1	< 0.001
20	Equal ratio	2-4	91.4	< 0.001
20	Equal ratio	3-4	34.2	< 0.001
20	High amensalism	1-2	108.4	< 0.001
20	High amensalism	1-3	147.2	< 0.001
20	High amensalism	1-4	129.6	< 0.001
20	High amensalism	2-3	71.9	< 0.001
20	High amensalism	2-4	80.8	< 0.001

Initial richness	Frequency of interaction types	Trophic level pair	Z statistic	p-value
20	High amensalism	3-4	29.2	< 0.001
20	High antagonism	1-2	131.4	< 0.001
20	High antagonism	1-3	170.1	< 0.001
20	High antagonism	1-4	160.2	< 0.001
20	High antagonism	2-3	77.3	< 0.001
20	High antagonism	2-4	97.9	< 0.001
20	High antagonism	3-4	40.6	< 0.001
20	High commensalism	1-2	120.5	< 0.001
20	High commensalism	1-3	157.7	< 0.001
20	High commensalism	1-4	138.7	< 0.001
20	High commensalism	2-3	73.2	< 0.001
20	High commensalism	2-4	83.4	< 0.001
20	High commensalism	3-4	30.6	< 0.001
20	High competition	1-2	112.8	< 0.001
20	High competition	1-3	154.5	< 0.001
20	High competition	1-4	135.9	< 0.001
20	High competition	2-3	76.7	< 0.001
20	High competition	2-4	85.6	< 0.001
20	High competition	3-4	30.2	< 0.001
20	High mutualism	1-2	112.3	< 0.001
20	High mutualism	1-3	170.6	< 0.001
20	High mutualism	1-4	158.5	< 0.001
20	High mutualism	2-3	89.3	< 0.001
20	High mutualism	2-4	103.5	< 0.001
20	High mutualism	3-4	38.4	< 0.001
40	Equal ratio	1-2	154.2	< 0.001
40	Equal ratio	1-3	169.5	< 0.001
40	Equal ratio	1-4	174.7	< 0.001
40	Equal ratio	2-3	77.3	< 0.001
40	Equal ratio	2-4	114.1	< 0.001
40	Equal ratio	3-4	54.9	< 0.001
40	High amensalism	1-2	148.3	< 0.001
40	High amensalism	1-3	154.0	< 0.001
40	High amensalism	1-4	160.7	< 0.001
40	High amensalism	2-3	68.9	< 0.001
40	High amensalism	2-4	104.6	< 0.001
40	High amensalism	3-4	51.0	< 0.001
40	High antagonism	1-2	218.2	< 0.001
40	High antagonism	1-3	220.1	< 0.001
40	High antagonism	1-4	231.5	< 0.001
40	High antagonism	2-3	83.9	< 0.001
40	High antagonism	2-4	138.9	< 0.001
40	High antagonism	3-4	71.5	< 0.001
40	High commensalism	1-2	155.5	< 0.001
40	High commensalism	1-3	176.5	< 0.001

Initial richness	Frequency of interaction types	Trophic level pair	Z statistic	p-value
40	High commensalism	1-4	169.3	< 0.001
40	High commensalism	2-3	82.5	< 0.001
40	High commensalism	2-4	108.7	< 0.001
40	High commensalism	3-4	47.8	< 0.001
40	High competition	1-2	146.7	< 0.001
40	High competition	1-3	152.7	< 0.001
40	High competition	1-4	157.9	< 0.001
40	High competition	2-3	70.2	< 0.001
40	High competition	2-4	103.3	< 0.001
40	High competition	3-4	48.5	< 0.001
40	High mutualism	1-2	140.5	< 0.001
40	High mutualism	1-3	190.6	< 0.001
40	High mutualism	1-4	195.2	< 0.001
40	High mutualism	2-3	99.7	< 0.001
40	High mutualism	2-4	135.4	< 0.001
40	High mutualism	3-4	61.1	< 0.001
60	Equal ratio	1-2	204.15	< 0.001
60	Equal ratio	1-3	194.8	< 0.001
60	Equal ratio	1-4	202.5	< 0.001
60	Equal ratio	2-3	86.9	< 0.001
60	Equal ratio	2-4	133.1	< 0.001
60	Equal ratio	3-4	66.6	< 0.001
60	High amensalism	1-2	174.8	< 0.001
60	High amensalism	1-3	163.0	< 0.001
60	High amensalism	1-4	172.1	< 0.001
60	High amensalism	2-3	74.6	< 0.001
60	High amensalism	2-4	115.6	< 0.001
60	High amensalism	3-4	58.4	< 0.001
60	High antagonism	1-2	337.6	< 0.001
60	High antagonism	1-3	267.2	< 0.001
60	High antagonism	1-4	287.2	< 0.001
60	High antagonism	2-3	82.8	< 0.001
60	High antagonism	2-4	161.8	< 0.001
60	High antagonism	3-4	91.2	< 0.001
60	High commensalism	1-2	182.9	< 0.001
60	High commensalism	1-3	178.4	< 0.001
60	High commensalism	1-4	182.8	< 0.001
60	High commensalism	2-3	82.4	< 0.001
60	High commensalism	2-4	121.8	< 0.001
60	High commensalism	3-4	59.7	< 0.001
60	High competition	1-2	190.0	< 0.001
60	High competition	1-3	164.7	< 0.001
60	High competition	1-4	182.3	< 0.001
60	High competition	2-3	72.9	< 0.001
60	High competition	2-4	121.9	< 0.001

Initial richness	Frequency of interaction types	Trophic level pair	Z statistic	p-value
60	High competition	3-4	63.5	< 0.001
60	High mutualism	1-2	173.3	< 0.001
60	High mutualism	1-3	203.3	< 0.001
60	High mutualism	1-4	212.3	< 0.001
60	High mutualism	2-3	103.8	< 0.001
60	High mutualism	2-4	146.6	< 0.001
60	High mutualism	3-4	67.2	< 0.001

Table A.3.2.7: Ratio of species with < 10 individuals and with > 100 individuals averaged over 100 assembled model communities.

Initial richness	Ratio abundant species	Ratio rare species
20	0.265	0.155
40	0.218	0.231
60	0.218	0.209

4. Additional figures
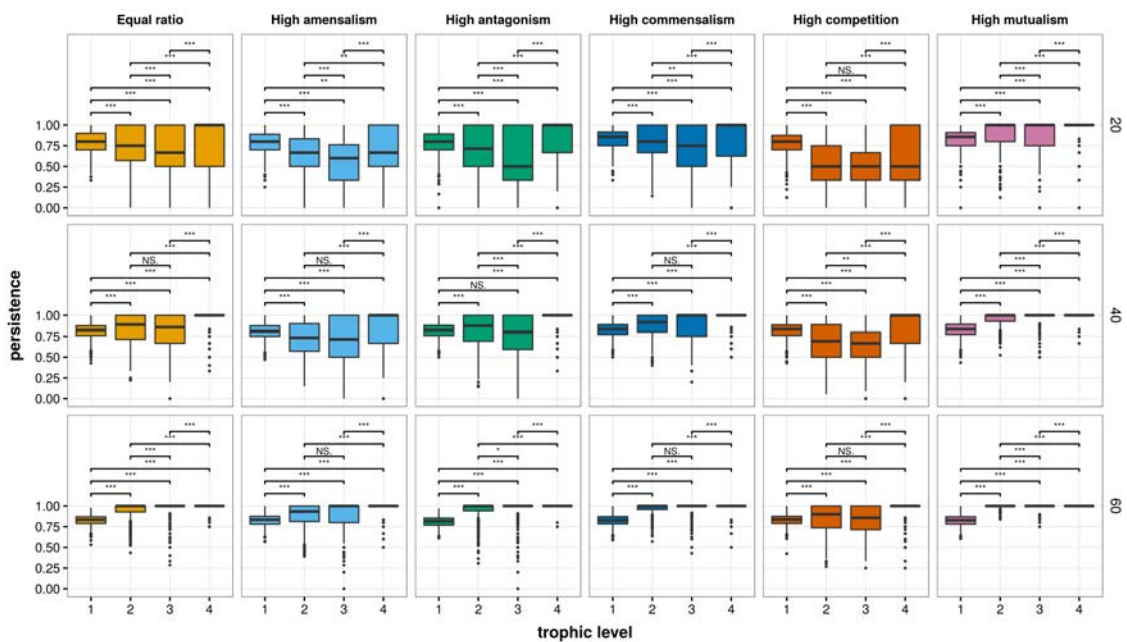
FIGURE A.3.2.1: Persistence values of the main simulations grouped by initial richness, interaction frequencies, and trophic level. The line inside the boxes represents the median values, lower and upper hinges correspond to the first and third quantiles and whiskers extend to the smallest/largest value no further than 1.5 times the inter-quartile range. Bars and symbols above the boxplots represent the outcome of Wilcoxon signed-rank tests (corrected for multiple comparisons with the Bonferroni correction) for the difference between pairs of groups (N.S: not significant, * p < 0.05, ** p < 0.01, *** p < 0.001).
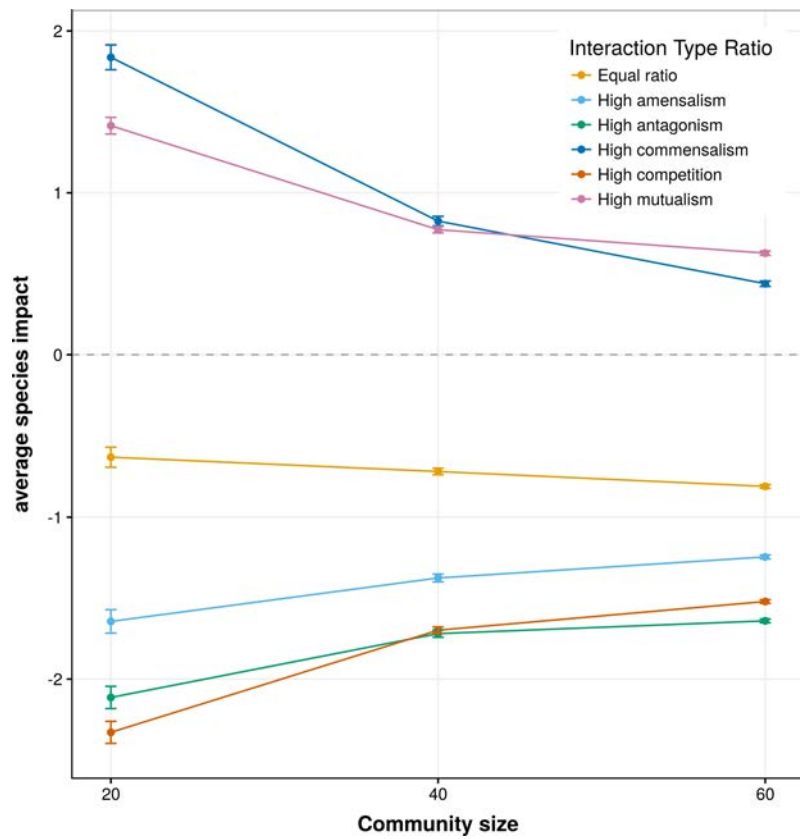
FIGURE A.3.2.2: Average pairwise species impact in model communities grouped by initial richness and interaction frequencies. Error bars represent standard error.

Appendix 3.3: Chapter 3 - Additional simulations and sensitivity analyses

Additional simulations

In order to evaluate the importance of the structural constraints imposed to our model communities, we performed a series of additional simulations in which we sequentally removed one of the three constraints evaluated. Here we briefly explain the details of each set of simulations.

1 - Uniform initial SAD: We relaxed the requisite of a skewed Species Abundance Distribution by the start of the simulations. We allowed species abundances to be randomly drawn from a uniform distribution with the only constraint that the summed value of abundances at each trophic level be lower than the initial number of species times 100.

2 - No trophic level scaling: In the main set of simulations, the overall initial abundance across trophic levels follows a power law with exponent 0.75 (see Methods in Chapter 3). We removed this scaling in this set of simulations and allowed trophic levels to be similar in initial abundances.

3 - No interaction structure: Here, we removed the distribution of interactions within and across trophic levels (Fig. 3.2 of Chapter 3). We only retained the topology of antagonistic interactions, in order not to obtain unrealistic configurations of basal species consuming predators. All other interaction types had the same probability of occurrence across same, adjacent or other trophic levels.

We performed these three sets of simulations for a subset of the initial richness and interaction frequency configurations, due to limitations in computing power. Specifically, we analyzed communities with initial richness of 20 and 40 species, and frequencies of equal ratio of interactions, high competition and high mutualism (an intermediate configuration and the ones displaying the most different behaviour). For each community type, we show the values of 1000 replicates. Here we replicate, for these configurations, Fig. 3.2, Fig. 3.3, Fig. 3.4 of Chapter 3, and Fig. A.3.2.1 of Appendix 3.2.
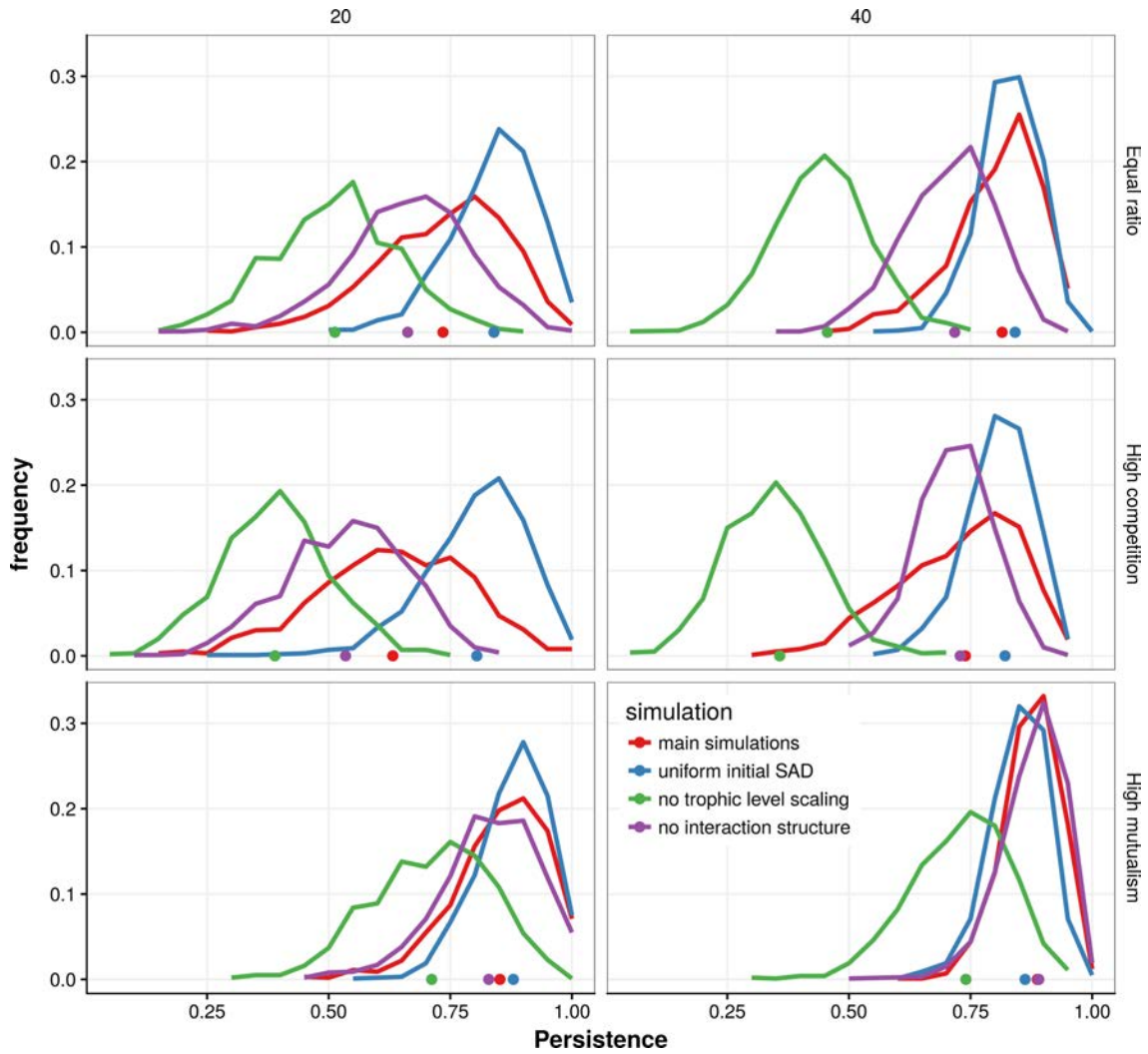
FIGURE A.3.3.1: Persistence ratios of the additional simulations. C.f. Fig. 3.2 of Chapter 3.
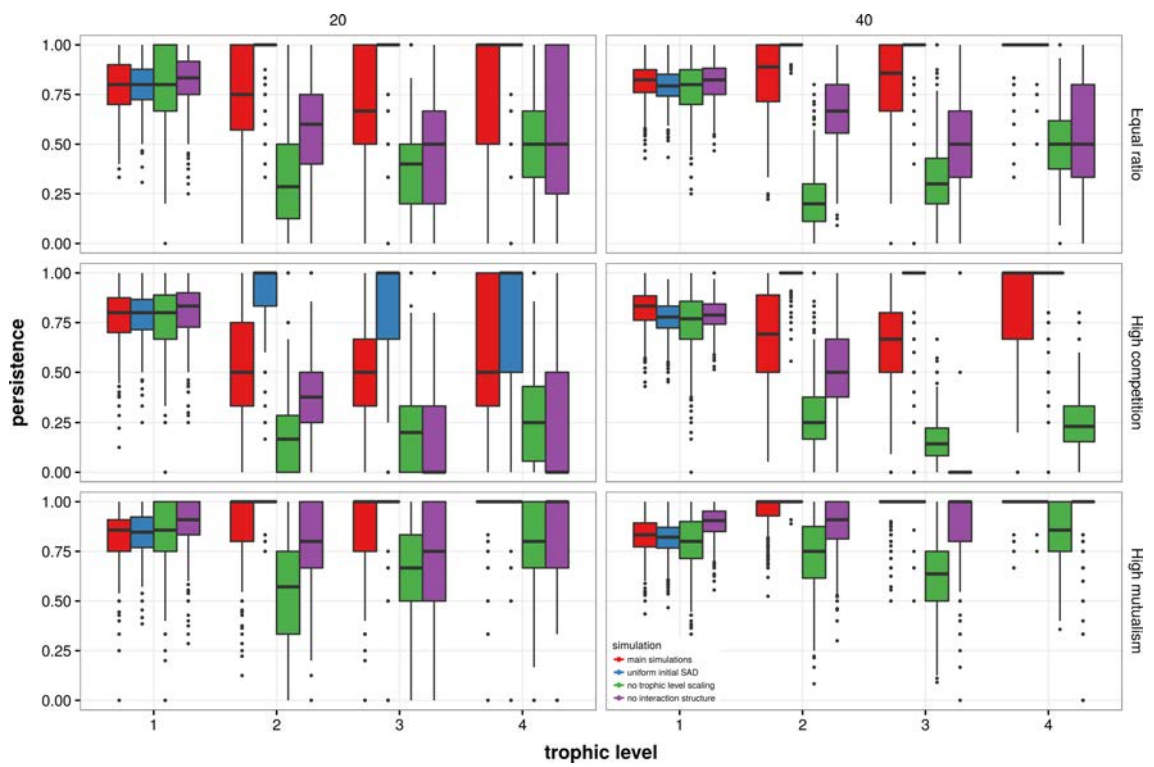
FIGURE A.3.3.2: Persistence ratios of the four different trophic levels for the additional simulations. C.f. Appendix 3.2: Fig. A.3.2.1
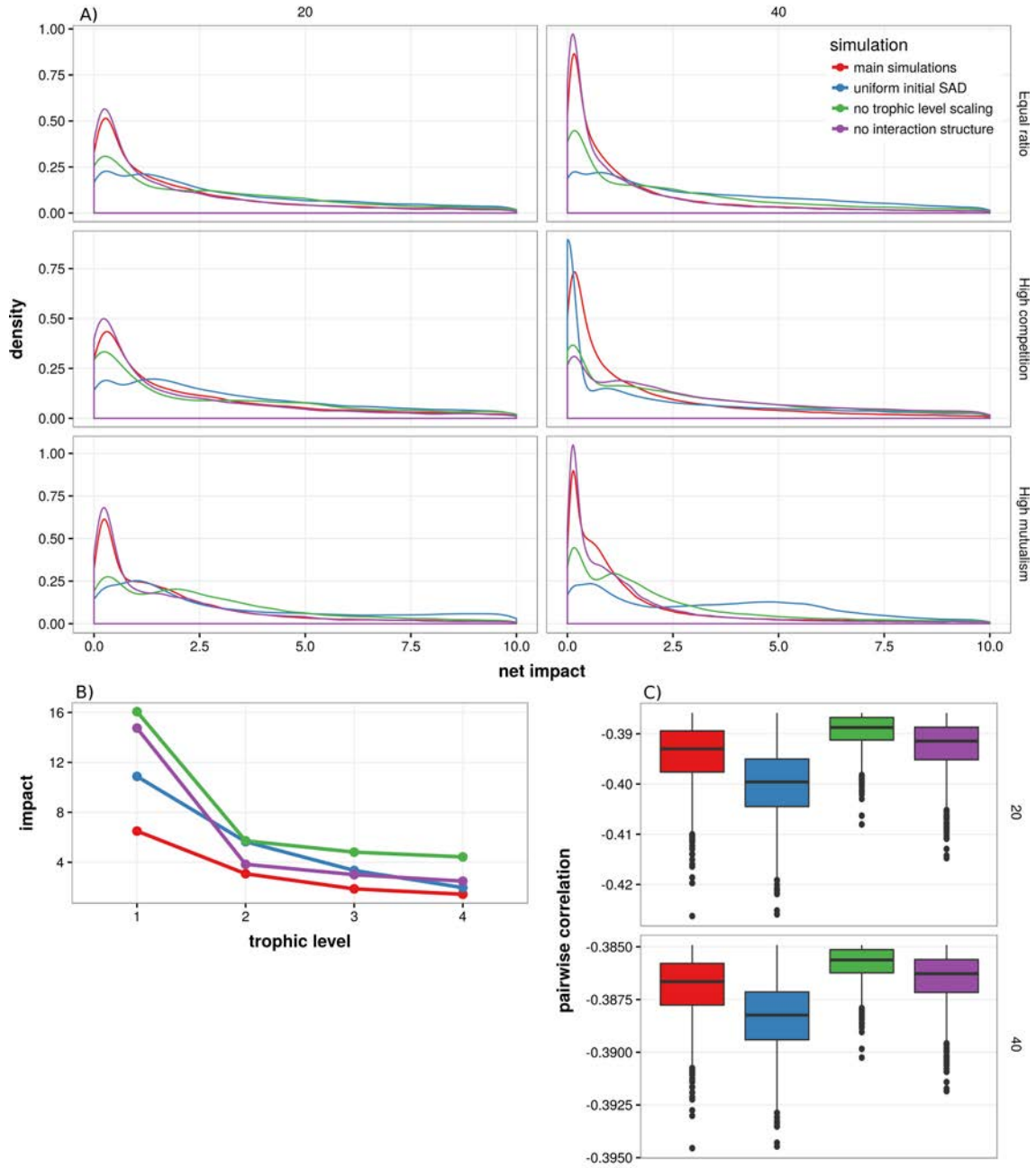
Figure A.3.3.3: Species impact and correlation patterns at the end of the additional simulations. C.f. Fig. 3.3 of Chapter 3.

Sensitivity analysis

We performed a partial sensitivity analysis on one of the parameters of the model in order to test its qualitative trends. The parameter selected is the scale factor k, that modulates the relative scale of a given per capita interaction: a higher k implies a higher per capita impact, up to the point that $k = 1$ produces per capita interactions that have the same order of magnitude as the intrinsic growth rates.

The motivation behind this parameter is to differentiate interactions by their per capita impact. For example, a single predator-prey interaction will generally have a higher per capita impact than any other single interaction, due to the death of the prey individual. Of course, there are exceptions to this scheme, so we checked the behaviour of our model by producing a small set of simulations with varying sets of k values.

A set of k values specifies the scaling factor for each of the five interaction types, e.g.:

$$k = (k_{amensalism}, k_{antagonism}, k_{commensalism}, k_{competition}, k_{mutualism})$$

The main simulations represent the hypothesis stated above, i.e. that antagonisms will generally have a higher per capita impact:

$$k_{main} = (0.1, 0.5, 0.1, 0.1, 0.1)$$

We generated three more sets of k values for this sensitivity analysis, thus obtaining a gradient from complete homogeneity in per capita impact (k_1) to the initial parameterization (k_4):

$$k_1 = (0.2, 0.2, 0.2, 0.2, 0.2)$$
$$k_2 = (0.167, 0.3, 0.167, 0.167, 0.167)$$
$$k_3 = (0.133, 0.4, 0.133, 0.133, 0.133)$$
$$k_4 = k_{main}$$

We tested the effect of the different sets of k in the dynamics of model communities with 20 species and three different configurations of interaction frequencies: an equal ratio of interactions, a high ratio of competition, and a high ratio of mutualism. We generated 500 replicates of each combination of initial richness, interaction frequencies and set of k values. Computational constraints prevented us from testing the effect of k over the complete set of community configurations, but the categories selected are representative of the whole set: communities with 20 species are, as shown in e.g. 3.2, the most sensitive to variations in the model parameters; in addition, the three configurations of interaction frequencies selected represent two extremes and an intermediate situation in regards to expected persistence. Therefore, we are moderately confident that the results from this sensitivity analysis can be representative of other configurations.

The results of the sensitivity analysis show that homogeneous k values across interaction types tend to increase persistence levels, for every configuration, and the differences between configurations are statistically significant in most cases (Fig. A.3.3.4). Statistical comparisons across groups were analyzed by performing Bonferroni-corrected pairwise Wilcoxon signed-rank tests on each pair of persistence values. It is also apparent that, regardless the set of k values chosen, communities with high proportion of mutualisms show the highest levels of persistence, while communities with high proportion of competition show the lowest levels. Therefore, the qualitative trends of the main simulations are maintained across different sets of interaction scaling factors.
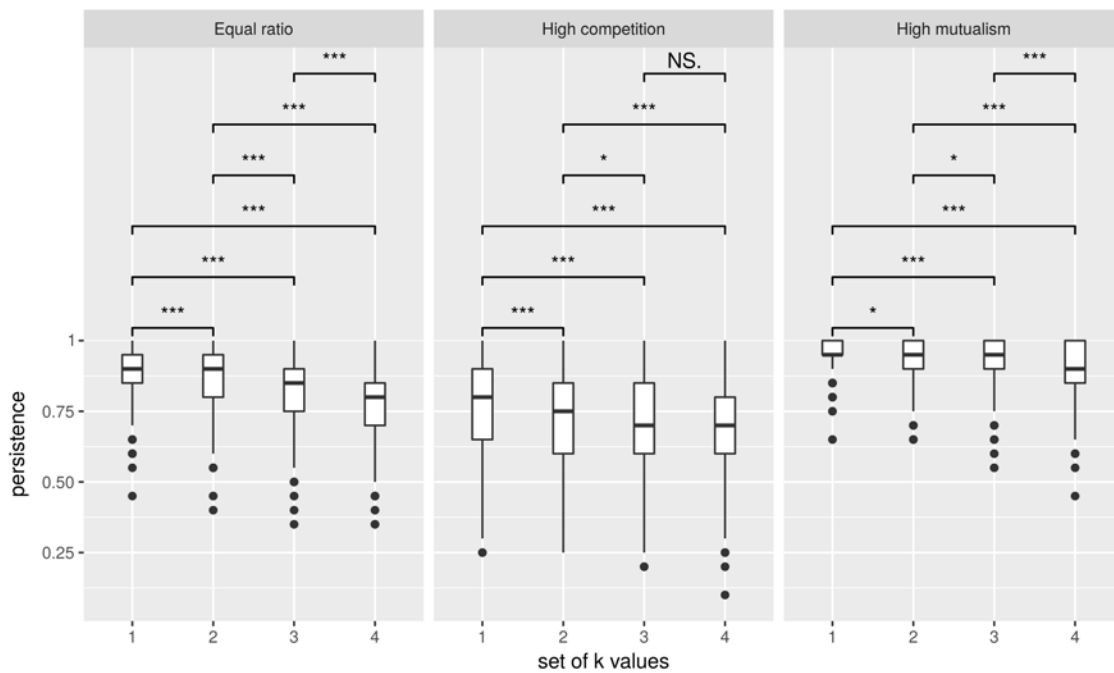

FIGURE A.3.3.4: Distribution of persistence values for 500 replicates of model communities parameterized with different sets of values for the scaling factor k. The x axis represents the different sets of values considered (see text). Bars above the boxplot represent the significance of each pairwise comparison (Wilcoxon signed-rank tests; * indicates $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Appendix 3.4: Chapter 3 - Network assembly, connectance, and interaction type ratio

Any set of interaction rules that prevents a pair of species from interacting modifies the connectance of the interaction network by an adjustment on the number of potentially feasible links. Connectance measured relative to a fully-connected network only makes sense if every pairwise interaction is potentially feasible. Otherwise, connectance should be computed relative to the potential number of links given the assembly contraints of the network. Linkage rules will vary among interaction types, so that in a multi-interaction network the potential number of links will be different for each sub-network.

Hence, specifying type-specific connectances and linkage rules, the probability that a given link is of a certain type can be obtained. For the sake of brevity, we name this set of probabilities the Interaction Type Ratio (ITR henceforth, where if a subscript is given, it indicates the probability of a certain interaction type). In the following example we demonstrate the difference between assuming a single value of connectance and setting type-specific connectances for network assembly, given the linkage probabilities of Fig. 3.1. These linkage probabilities can be summarised qualitatively in that for commensalism and mutualism, every pairwise link is allowed, while amensalism can only occur between species of the same trophic level, antagonism does not occur in a bottom-up fashion (i.e. where the species from the lower level benefits to the expense of a species of an upper level), and competition only occurs between species of the same or adjacent levels.

Assume a network with $N = 20$ nodes. If no link is structurally forbidden when we consider the overall network, the potential number of links is:

$$S = N(N-1)/2 = 190$$

Furthermore, imposing an overall connectance $C = 0.2$ and equal ITR, i.e. $ITR_x = 0.2$ for every interaction type x, yields the following number of realised links:

$$L = C * S = 38, L_x \approx 8$$

With these numbers, we may calculate the specific connectances of every interaction type for this particular network. Take as an example a community

generated with the constraints and parameterization stated in chapter 3 and in Appendix 3.1 (e.g. four discrete trophic levels, abundance scaling across trophic levels, 2000 individuals at the basal trophic level). The linkage rules can be expressed mathematically to obtain the number of potential links per interaction type. The scaling constraints predict that, on average, the distribution of the N species in the $T = 4$ trophic levels will be $\{N_1 = 7, N_2 = 6, N_3 = 4, N_4 = 3\}$. Then:

$$S_{amensalism} = \sum_{i=1}^{T} \frac{N_i(N_i - 1)}{2} = 49$$

$$S_{antagonism} = N(N - 1)/2 = 190$$

$$S_{commensalism} = N(N - 1)/2 = 190$$

$$S_{competition} = \sum_{i=1}^{T} \frac{N_i(N_i - 1)}{2} + \sum_{j=1}^{T-1} N_j * N_{j-1} = 123$$

$$S_{mutualism} = N(N - 1)/2 = 190$$

Hence, the type-specific connectances are:

$$C_{amensalism} = L_{amensalism}/S_{amensalism} = 0.163$$

$$C_{antagonism} = L_{antagonism}/S_{antagonism} = 0.042$$

$$C_{commensalism} = L_{commensalism}/S_{commensalism} = 0.042$$

$$C_{competition} = L_{competition}/S_{competition} = 0.065$$

$$C_{mutualism} = L_{mutualism}/S_{mutualism} = 0.042$$

By definition, type-specific connectances will be lower than the overall connectance. Only in the unrealistic scenario of networks with a single interaction type, its specific connectance will equal the overall connectance, while all the other types will have a specific connectance of zero. As overall connectance increases, more links are realised for each interaction type, and type-specific connectances will increase in turn. Fig. A.3.4.1 shows the variation in type-specific connectances as overall connectance increases for networks in which interactions are realised with equal probability for each interaction type.

Note how the ratio between type-specific connectance and overall connectance varies with the type of interaction. This is a direct consequence of the linkage rules that define the set of potential links available to each interaction type: smaller sets of potential links necessarily yield higher connectances for the same number of realised links. Also, given the set of linkage rules chosen, it is not possible to obtain networks of $ITR_x = 0.2, \forall x$ and overall connectance on the range of $C \geq 0.6$. In this case, this is due to the fact that amensalistic interactions occurr only between species of the same trophic level, and assuming that any two species cannot interact in more than one way, these links can potentially be 'filled' by any other interaction type. Therefore, an upper limit to the amensalistic
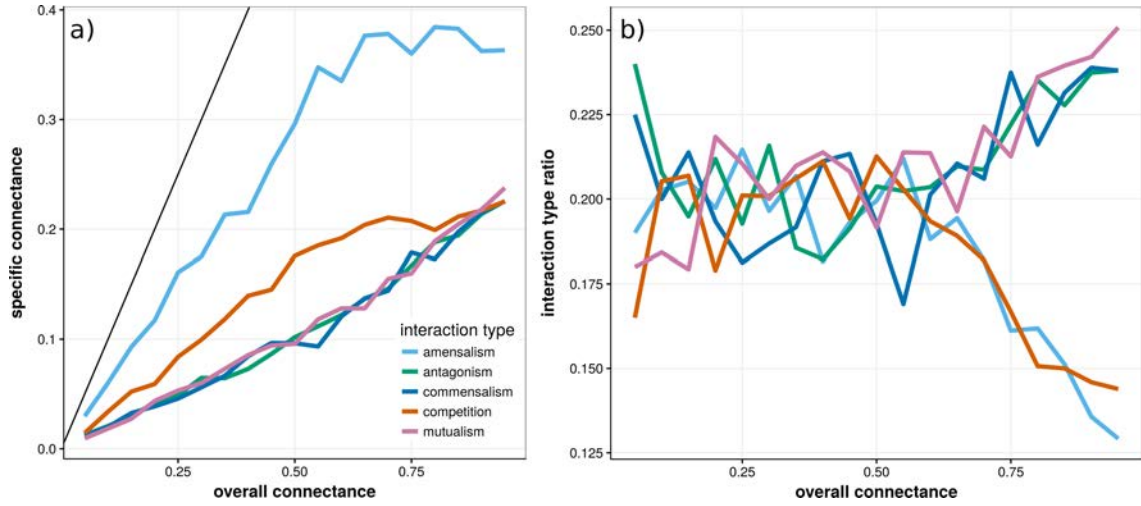
Figure A.3.4.1: relationship between overall connectance and a) specific connectances of each type, b) ITR. Black line in panel a) shows the y=x line

realised interactions is imposed not only by its ITR, but also by the occurrence of other interaction types. Once this limit is reached for amensalistic interactions, other interaction types, however, still maintain part of their potential link space unoccupied, and therefore can keep increasing in number of links, connectance and, hence, ITR.

If, instead of imposing a constant ITR, we assemble networks with fixed specific connectances, the overall connectance and ITR will vary accordingly. As in the example above, assume a network with $N = 20$ nodes, the same linkage rules and, therefore, same potential number of links per interaction type. In this case, setting $C_x = 0.2 \forall x$ yields the following approximate number of links:

$$L_{amensalism} = C_{amensalism} * S_{amensalism} = 9$$
$$L_{antagonism} = C_{antagonism} * S_{antagonism} = 38$$
$$L_{commensalism} = C_{commensalism} * S_{commensalism} = 38$$
$$L_{competition} = C_{competition} * S_{competition} = 25$$
$$L_{mutualism} = C_{mutualism} * S_{mutualism} = 38$$

$$L = \sum_x L_x = 148$$

and ITR:

$$ITR_{amensalism} = L_{amensalism}/L = 0.06$$
$$ITR_{antagonism} = L_{antagonism}/L = 0.257$$
$$ITR_{commensalism} = L_{commensalism}/L = 0.257$$
$$ITR_{competition} = L_{competition}/L = 0.166$$
$$ITR_{mutualism} = L_{mutualism}/L = 0.257$$

Not surprisingly, ITRs are not equivalent to specific connectances, given that the potential link set is different for each interaction type. The value of overall connectance for this network is:

$$C = \frac{\sum_x L_x}{S} = 0.78$$

As specific connectance values increase, overall connectance quickly reaches 1 (Fig. A.3.4.2). Once this threshold is crossed, increases in specific connectance are no longer reflected in the assembled network, and in fact, an increasing number of links cannot be realised. Therefore, assuming that most interactions are allowed (i.e. not structurally forbidden), as in the linkage rules used here, specific connectances as low as ≈ 0.25 for every interaction type already fill the entire set of potential links. These numbers apply to binary connectances, that consider only the presence or absence of a given interaction. If quantitative interactions are available, weighted connectances can be obtained, and these will better reflect the effective number of links (Ulanowicz et al., 2014).
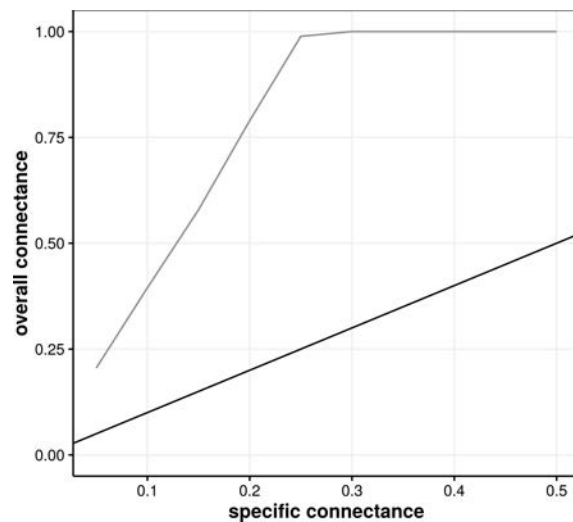

FIGURE A.3.4.2: relationship between specific connectances and overall connectance, assuming equal specific connectances for each interaction type. Black line shows the y=x line. Note that axes are switched with respect to Fig. A.3.4.1, for reflecting the behaviour of the overall connectance.

Appendix 4.1: Chapter 4 - Supplementary results

Supplementary tables

Table A.4.1.1: Differences in evenness between pairs of trophic guilds in the empirical datasets, as given by the beta regression detailed in Table 4.3 of chapter 4.

contrast	Estimate	Std. Error	df	z ratio	p-value
plants - herbivores	-0.868	0.054	Inf	-15.882	< 0.05
plants - omnivores	-0.753	0.063	Inf	-11.975	< 0.05
plants - carnivores	-0.712	0.069	Inf	-10.382	< 0.05
herbivores - omnivores	0.115	0.05	Inf	2.315	0.0947
herbivores - carnivores	0.157	0.061	Inf	2.567	0.0503
omnivores - carnivores	0.042	0.068	Inf	0.614	0.927

Table A.4.1.2: Differences in skewness between pairs of trophic guilds in the empirical datasets, as given by the multinomial regression detailed in Table 4.2 of chapter 4.

contrast	Estimate	Std. Error	df	t ratio	p-value
category = [-0.5,0.5]:					
plants - herbivores	-0.216	0.066	10	-3.269	< 0.05
plants - omnivores	-0.343	0.072	10	-4.761	< 0.05
plants - carnivores	-0.205	0.078	10	-2.623	< 0.05
herbivores - omnivores	-0.126	0.047	10	-2.666	0.0930
herbivores - carnivores	0.011	0.053	10	0.215	0.9963
omnivores - carnivores	0.138	0.063	10	2.195	0.1898
category = (0.5,1]:					
plants - herbivores	0.216	0.066	10	3.269	< 0.05
plants - omnivores	0.343	0.072	10	4.762	< 0.05
plants - carnivores	0.205	0.078	10	2.623	0.0994
herbivores - omnivores	0.127	0.047	10	2.666	0.0930
herbivores - carnivores	-0.011	0.053	10	-0.215	0.9963
omnivores - carnivores	-0.138	0.063	10	-2.195	0.1899
category = [-1,-0.5):					
plants - herbivores	$-5.4*10^{-6}$	$3*10^{-5}$	10	-0.179	0.9978
plants - omnivores	$-2.8*10^{-6}$	$1.6*10^{-5}$	10	-0.174	0.9980
plants - carnivores	$-1.8*10^{-5}$	$1*10^{-4}$	10	-0.178	0.9979
herbivores - omnivores	$2.6*10^{-6}$	$1.5*10^{-5}$	10	0.176	0.9979
herbivores - carnivores	$-1.3*10^{-5}$	$7.4*10^{-5}$	10	-0.177	0.9979
omnivores - carnivores	$-1.5*10^{-5}$	$8.8*10^{-5}$	10	-0.178	0.9979

Table A.4.1.3: Differences between the proportion of species and individuals of the mammal trophic guilds, analyzed via Wilcoxon signed-rank paired tests.

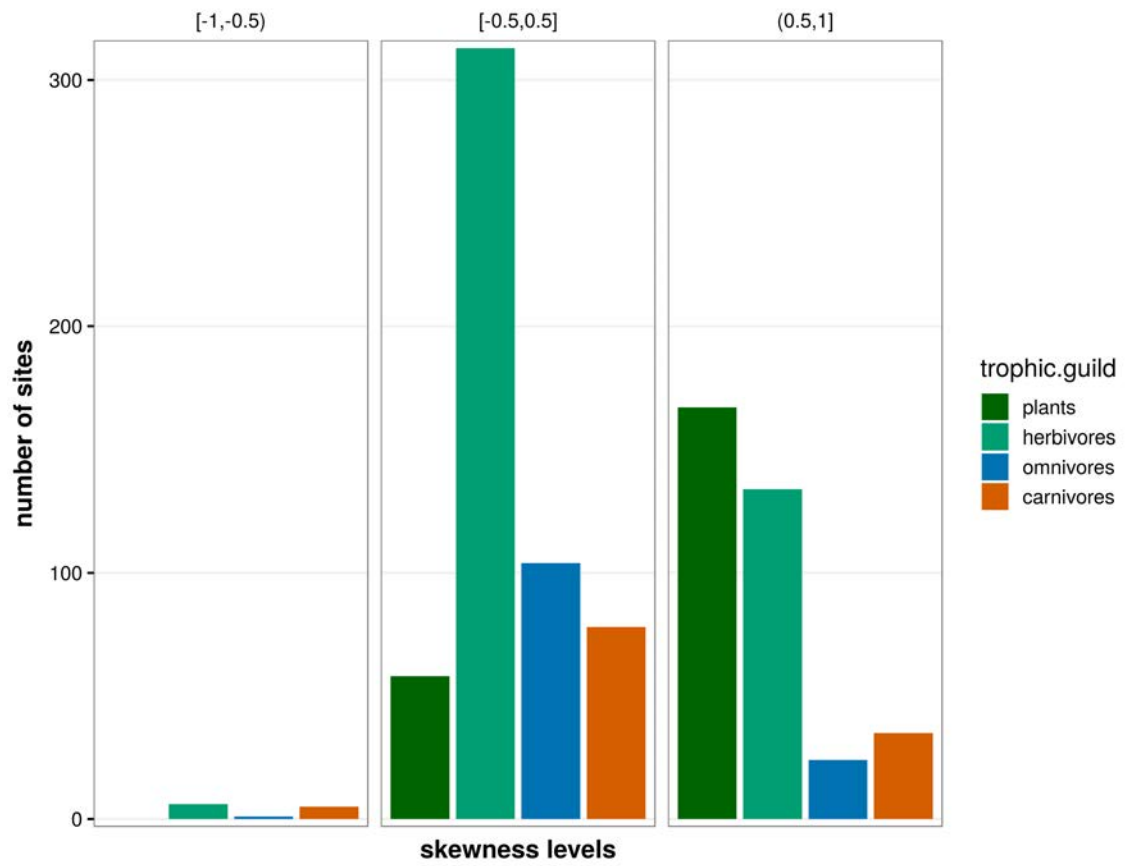| trophic guild	mean sp	s.d. sp	mean ind	s.d. ind	W	p-value
herbivores	0.623	0.216	0.607	0.324	131422	0.144
omnivores	0.330	0.198	0.408	0.313	162226	< 0.05
carnivores	0.305	0.179	0.211	0.244	18772	< 0.05

Supplementary figures

Figure A.4.1.1: Skewness levels observed in empirical datasets

Appendix 5.1: Chapter 5 - Supplementary results

Here we show the response of the studied metrics in relationship to variability in the dispersal and foraging rates (d and f, which are both fixed to 0.5 in the main simulations). We performed supplementary simulations in which we varied both rates in the interval $[0.25, 0.75]$. In the simulations accounting for both dispersal and foraging, we also simulated communities with high values of dispersal rates and low foraging rates, and viceversa.

The ratio of positive to negative interactions (left panel of Fig. A.5.1.1) varies from 0.94 to 1.05, with the highest variability being observed in the inter-patch effects of the dispersal simulation and the intra-patch effects of the foraging one. The magnitude of the net effects is much more variable for intra-patch effects than for inter-patch ones (middle panel of Fig. A.5.1.1), with its average value being in all cases relatively close to zero, which invites the interpretation that, regardless of the parameterization chosen, positive and negative net effects tend to mirror each other in number and also in magnitude. The number of pairwise interactions that switch sign from direct to net effect (right panel of Fig. A.5.1.1) is lowest in the dispersal simulations, but these also show the highest variability, in the local, intra-patch, interactions. Simulations with foraging and with both movement types are less variable and, in all cases, the frequency of sign switches between populations of different locations is lower than the frequency of switches between populations of the same location.

The variations in d and f are reflected in the relationship between the magnitude of intra and inter-patch net effects (Fig. 5.2). In the dispersal simulations, an increase in d trigger an increase in inter-patch net effects relative to intra-patch ones (Fig. A.5.1.2, three upper panels). In the foraging configuration, higher inter-patch foraging triggers a higher variability in both intra-patch and inter-patch effects, with no apparent directionality, whereas low f values clearly reduce the magnitude of inter-patch effects, as expected. The simulations with both dispersal and foraging show a mixture of the patterns described above; it is worth noting that even a small addition of foraging is able to scatter the packed configuration of dispersal-only net effects of the upper panels of Fig. A.5.1.2.

The spatial decay of net effects is quite similar across parameterizations (Fig. A.5.1.3 and Fig. A.5.1.4). Interestingly, for high values of inter-patch dispersal or foraging, the spatial cascades do not generally increase in length or in the magnitude of the effect at a given length (compare middle and right panels of Fig. A.5.1.3 and Fig. A.5.1.4). On the other hand, low values of d or f do induce
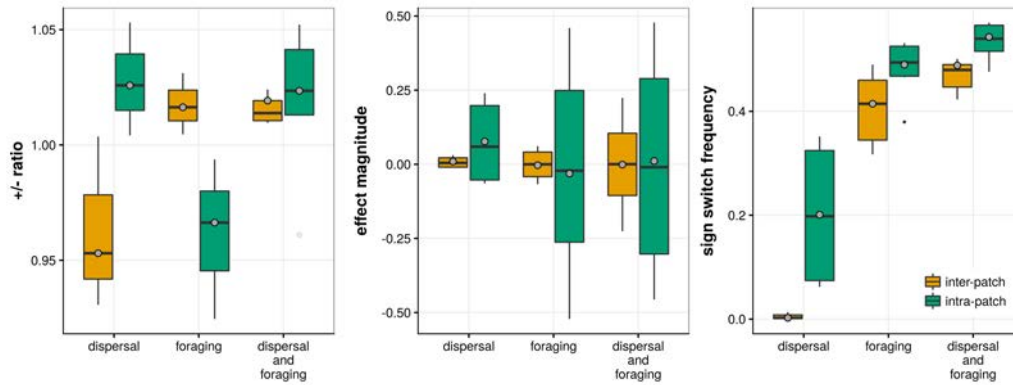
FIGURE A.5.1.1: Variability in a) ratio of positive to negative net effects, b) mean net effect magnitude, and c) relative frequency of sign switches between direct and net effects, for varying dispersal and foraging rates. Grey points represent the metrics for the values of the main simulations (d = 0.5, f = 0.5) .

lower net effects across the spatial cascades generated (compare middle and left panels of Fig. A.5.1.3 and Fig. A.5.1.4, note the variation in vertical axis). This asymmetrical effect could be due to the design and parameterization of the model or reflect an underlying ecological process of effect dampening at high direct interaction strengths.
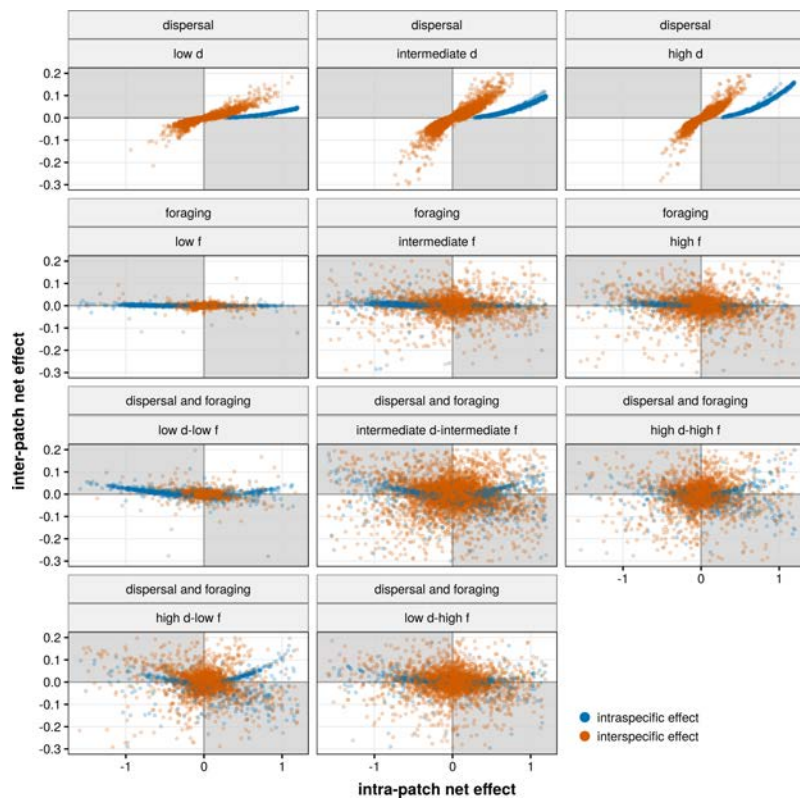
Figure A.5.1.2: Variability in across and within-patch pairwise net effects for different dispersal and foraging rates (cf Fig. 5.2 of chapter 5). In the panels, "d" is the dispersal rate, "f" foraging rate, "low" indicates a value of 0.25, "intermediate" 0.5, and "high" 0.75. Note that "intermediate" values correspond to the parameterization of the main simulations.
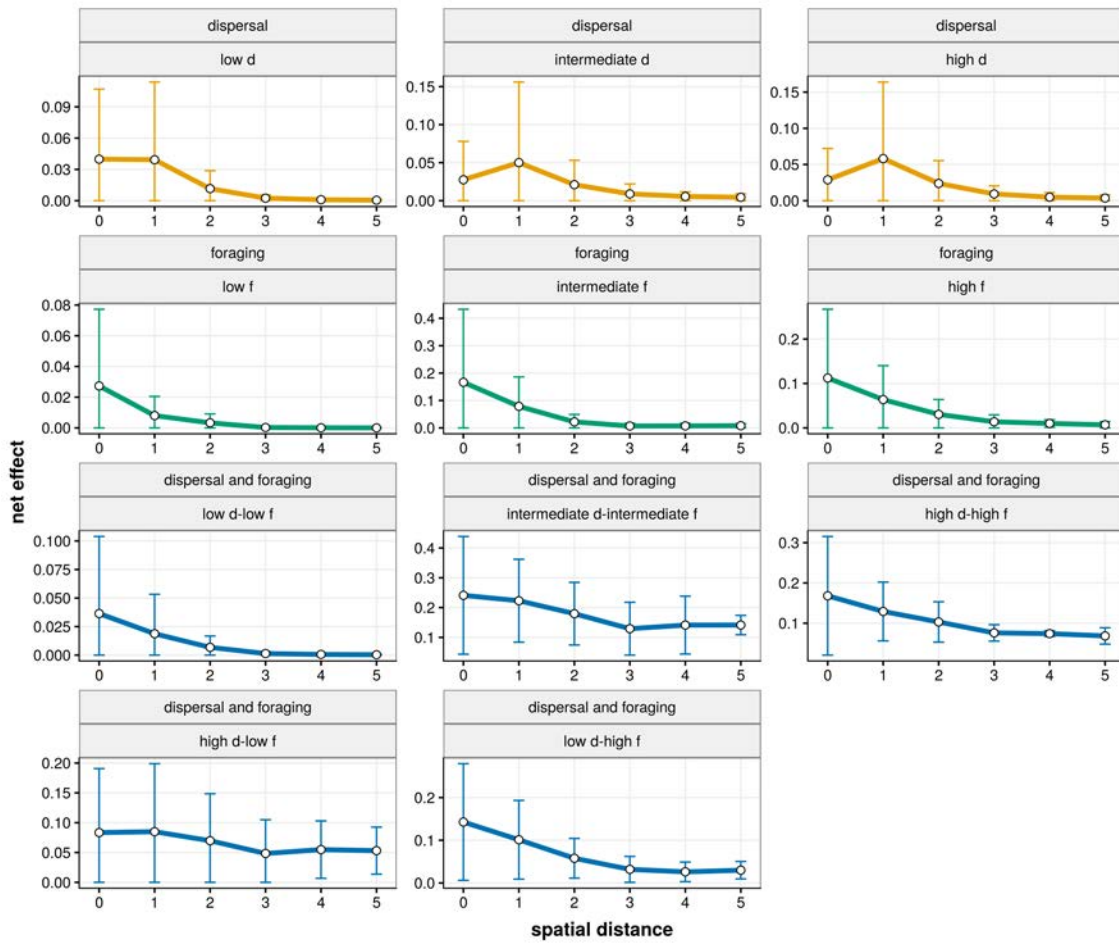
FIGURE A.5.1.3: Variability in the relationship between net effect and spatial distance for different dispersal and foraging rates (cf panel a of Fig. 5.3 in chapter 5). Panel legend as in Fig. A.5.1.2
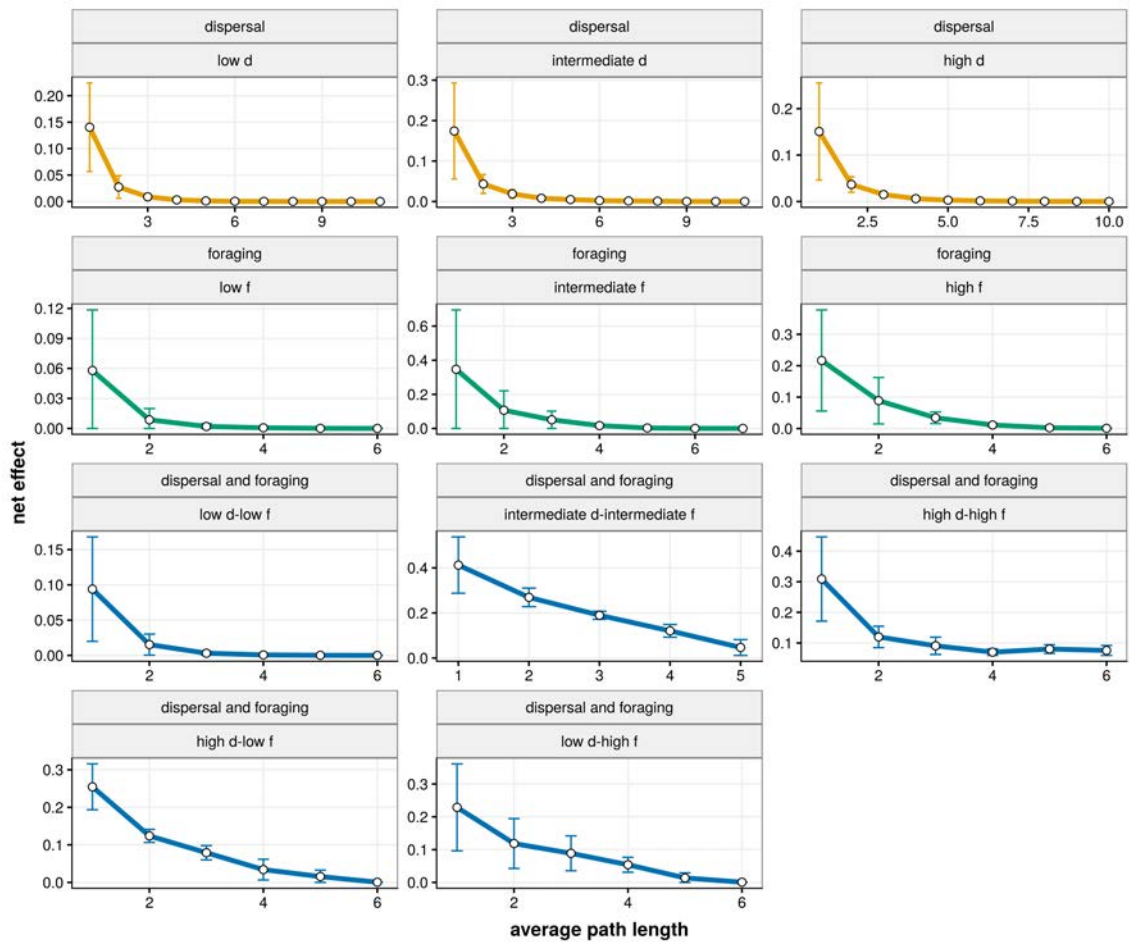
Figure A.5.1.4: Variability in the relationship between net effect and average path length for different dispersal and foraging rates (cf. panel (b) of Fig. 5.3 in chapter 5). Panel legend as in Fig. A.5.1.2

Appendix 6.1: Chapter 6 - Physiological response curves and additional results

We modelled the physiological response of species to a non-resource environmental factor following the conceptual hypothesis of Maestre et al. (2009), who assumed that plant species are ordered on a continuum ranging from pure competitors to pure stress-tolerants. Species were able to randomly colonize locations alongside an environmental gradient with varying levels of both non-resource and resource environmental factors (Fig. A.6.1.1). Competitive species survive and grow best in optimal conditions, but are very sensitive to environmental stress. Stress-tolerant species, on the other hand, maintain moderate levels of survival and growth for higher stress levels.

For implementing this framework, we derived a flexible function able to reproduce different functional responses. The function is

$$P(x) = \frac{k * p_0 * e^{r_1 x}}{k + p_0 * e^{r_1 x - 1}} - c(e^{r_2 x - 1}) \tag{7.11}$$

where P(x) is the response variable, that in our scenario corresponds to survival or growth probability. The parameterisation we obtained for the species at the ends of the continuum, mimicking Fig. 1 of Maestre et al. (2009), is given in Table A.6.1.1. With that parameterisation at the extreme behaviours, we generated 20 response curves for model species (Fig. A.6.1.2), such that the transition between pure competitors and pure stress tolerant species is smooth, and all species have maximum survival probability in the absence of environmental stress.

Table A.6.1.1: Parameterisation of 7.11 for purely competitive and purely stress-tolerant species. Intermediate species have parameters within these ranges in all cases.

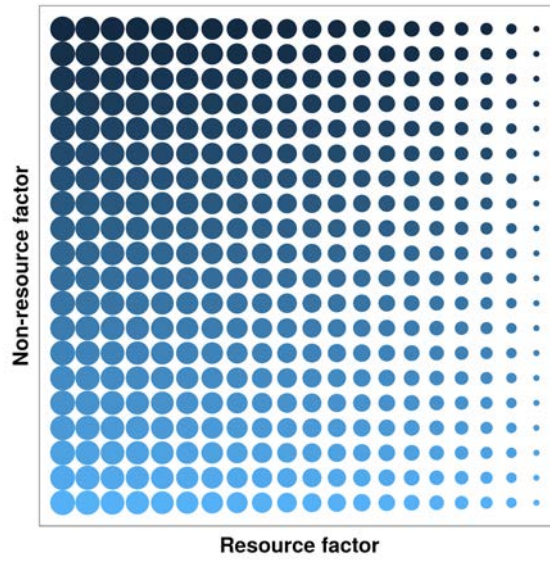|	survival		growth	
	stress-tolerant	competitor	stress-tolerant	competitor
k	1	0.1	0.7	0.1
p_0	1	1	0.7	1
r_1	0.1	0.01	0.1	0.05
r_2	1	0.85	0.5	0.5
c	$3 * 10^{-5}$	$3 * 10^{-4}$	$5 * 10^{-3}$	0.05

FIGURE A.6.1.1: A series of locations with linearly varying conditions of a resource factor (represented by circle size) and non-resource factor (from light to dark blue). The grid represented in this figure is of size 20*20, whereas the one used in the model is of size 50*50.
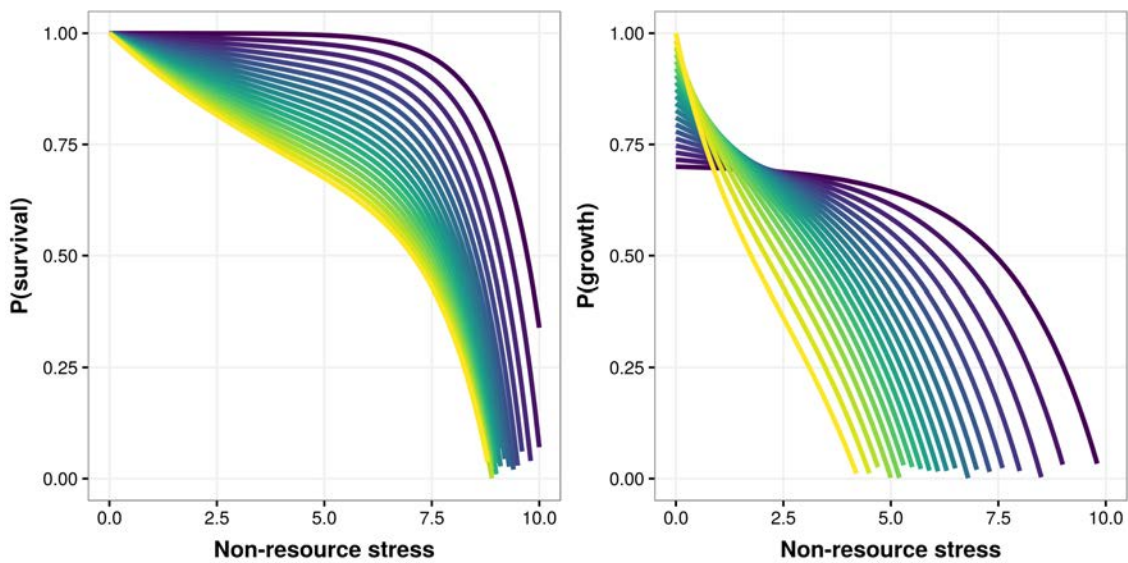

FIGURE A.6.1.2: Physiological response curves of 20 modelled species to a single non-resource environmental factor. Probabilities of survival (left panel) and growth (right panel) are modelled, and species range from purely stress-tolerant (dark blue curves) to purely competitive (yellow curves). Stress-tolerant species maintain a high probability of survival under a higher range of environmental stress, and also keep a moderate growth probability for longer than competitive species. The latter, on the other hand, are very sensitive to environmental stress, but grow better than stress-tolerant species under ideal conditions. These functional responses are adapted from Fig. 1 of **Maestre et al. (2009)**
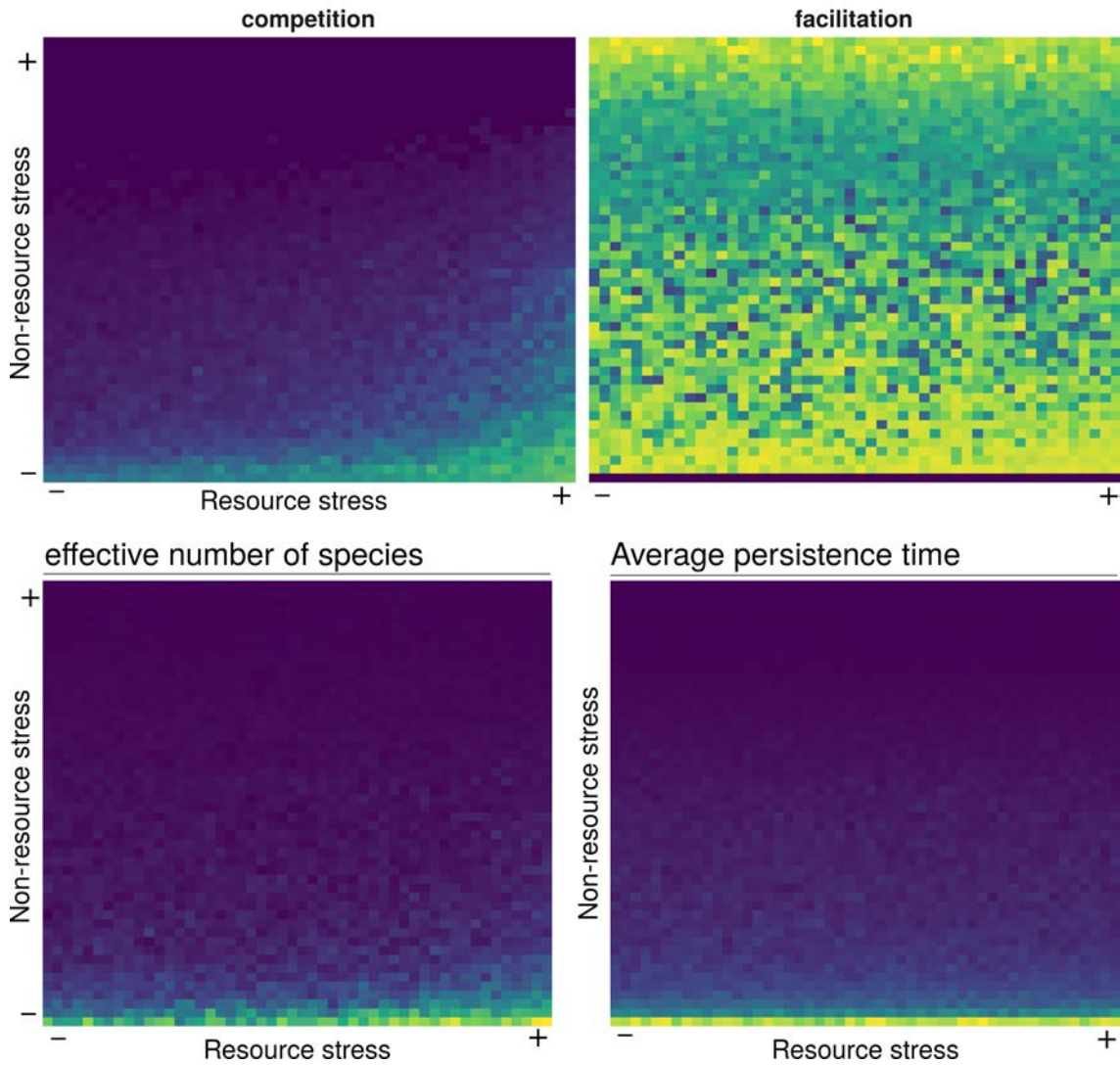
Figure A.6.1.3: Variation in community-level properties across the two dimensional gradient. As we are not interested in absolute values but rather in trends of variation, values in all panels are normalised, ranging from 0 (minimum values, dark blue) to 1 (maximum values, yellow).
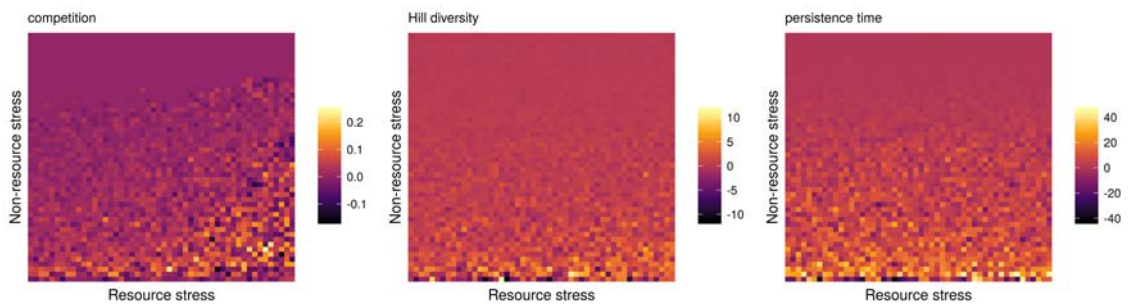

Figure A.6.1.4: Distribution of the net differences between simulations with or without facilitation. Bright colours indicate high values of a metric in the simulations with facilitation relative to the ones without facilitation, and viceversa for darker shades. Note that the colour scales in the three panels are not equivalent; this is due to the different ranges of the differences among metrics.

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