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What does a bioenergetic network approach tell us about the functioning of ecological communities?

par

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RÉSUMÉ

Les perturbations auxquelles font face les communautés écologiques, du fait des activités humaines, sont à l'origine de changements profonds dans ces communautés. Nombreuses caractéristiques des espèces sont altérées, de leur physiologie à leur occurrence même. Ces changements se répercutent sur la composition, la diversité et la structure des communautés, puisque les espèces n'interagissent pas tout le temps de la même manière en fonction des conditions. Prévoir le devenir de ces communautés émergentes, et des fonctions qu'elles soutiennent est un défi central de l'écologie et de nos sociétés.

Différents cadres conceptuels ont été utilisés pour relever ce défi, basés sur différents mécanismes écologiques, et ont divergé en plusieurs domaines. D'un côté, l'analyse des chaînes trophiques utilise la consommation pour expliquer les effets de la diversité verticale (le nombre de niveaux trophiques) sur le fonctionnement, et de l'autre côté, les analyses biodiversité-fonctionnement lient compétition et effets de la diversité horizontale (la diversité au sein des niveaux trophiques isolés). Chacun de ces domaines a produit des résultats clés pour comprendre les conséquences fonctionnelles des changements de composition et diversité des communautés écologiques. Cependant, ils sont chacun basés sur différentes simplifications fortes des communautés.

L'hypothèse qui sous-tend cette thèse est que la réconciliation en un même cadre de travail des résultats fondamentaux de ces champs conceptuels divergents, ainsi que des effets des changements de structure de la biodiversité, est une étape clé pour pouvoir améliorer notre compréhension du fonctionnement de communautés écologiques en changement.

L'essor récent des méthodes d'analyse des réseaux trophiques, et des modèles permettant de simuler le fonctionnement de ces réseaux trophiques offre un cadre idéal pour cette réconciliation. En effet, les réseaux trophiques cartographient les échanges de matière entre toutes les espèces d'une communauté, permettant la mise en place d'interactions variées. Ils reflètent mieux la réalité complexe des communautés que les chaînes trophiques ou leurs

niveaux trophiques isolés en intégrant notamment compétition et consommation. Un modèle ressource-consommateur bioénergétique classique, développé par Yodzis et Innes (1992), permet d'en simuler le fonctionnement, en intégrant des mécanismes et taux testés empiriquement.

Au-delà d'utiliser ces outils, cette thèse se concentre aussi sur leur évaluation. Après un premier chapitre d'introduction, le second chapitre propose une plateforme ouverte, commune, solidement testée et efficace pour l'utilisation du modèle bioénergétique, permettant ainsi une synthèse plus rapide et aisée des résultats. Le troisième chapitre est une revue du corpus méthodologique d'analyse des réseaux trophiques, proposant une gamme de méthodes robustes et informatives, et soulignant leur domaine d'application et leurs limites. Enfin le quatrième chapitre met ce cadre méthodologique à l'épreuve. Dans ce chapitre, nous montrons l'existence d'une relation entre la complexité de la structure du réseau trophique des communautés et leur régime de fonctionnement, se traduisant par la réalisation de différentes prédictions issues de l'analyse des chaînes trophiques ou des analyses diversité-fonctionnement. Cette mise en évidence des conditions structurelles pour la réalisation de différentes prédictions nous permet de mieux comprendre quels mécanismes écologiques prédominent selon différentes conditions, dirigeant l'effet de la diversité sur le fonctionnement.

MOTS CLEFS

-Dynamiques de biomasse

-Écologie des communautés

-Écologie computationelle

-Fonctionnement des communautés

-Modèle bioénergétique

-Modèle consommateur-ressource

-Relations allométriques

-Réseaux trophiques

-Théorie des graphes

ABSTRACT

Human-driven disturbances are causing profound changes in ecological communities, as many characteristics of species are altered, from their physiology to their very occurrence. These changes affect the composition, diversity and structure of communities, since species do not always interact in the same way under different conditions. Predicting the fate of these emerging communities, and the functions they support, is a central challenge for ecology and our societies.

Diverging conceptual frameworks have been used to address this challenge, based on different ecological mechanisms. On the one hand, food chain analysis uses consumption to explain the effects of vertical diversity (the number of trophic levels) on functioning, and on the other hand, biodiversity-functioning analyses link competition and the effects of horizontal diversity (diversity within isolated trophic levels). Each of these domains has produced key results for understanding the functional consequences of changes in the composition and diversity of ecological communities. However, they are each based on different strong simplifications of communities.

The hypothesis underlying this thesis is that reconciling the fundamental results of these divergent conceptual fields, as well as the effects of changes in the structure of biodiversity, into a single framework is a key step towards improving our understanding of the functioning of changing ecological communities.

The recent development of food web analysis and of models to simulate food webs functioning provides an ideal framework for this reconciliation. Food webs map the exchange of matter between all species in a community, allowing for a variety of interactions to take place. They better reflect the complex reality of communities than food chains or their isolated trophic levels, notably by integrating competition and consumption. A classical consumer-resource bioenergetic model developed by Yodzis and Innes (1992) specifically makes it possible to realistically simulate their functioning, using empirically tested mechanisms and rates.

Beyond using these tools, this thesis focuses on their evaluation and implementation. After a first, introductory chapter, the second chapter proposes an open, common, well-tested and efficient platform for the use of the bioenergetic model, allowing a faster and easier synthesis of the results. The third chapter is a review of the methodological corpus for ecological networks analysis, outlining a range of robust and informative methods, and highlighting their scope and limitations. Finally, the fourth chapter puts this methodological framework to the test. In this chapter, we show the existence of a relationship between the complexity of communities' food-web structure and functioning regime, resulting in the realization of different predictions from food chain analysis or diversity-functioning analyses. This demonstration of the structural conditions for the realization of different predictions allows us to better understand which ecological mechanisms predominate under different conditions, directing the effect of diversity on functioning.

KEYWORDS

-Allometric scaling

-Bioenergetic model

-Biomass dynamics

-Community ecology

-Community functioning

-Computational ecology

-Consumer-resource model

-Food webs

-Graph theory

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ACRONYMS

- BEF: Biodiversity-Ecosystem Functioning
- BEFWm: Bio-Energetic Food-Web model
- ADBm: Allometric Diet Breadth model
- IGP: Intra-Guild Predation

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Foreword

The study of organisms and how they interact with one another and with their environment to form integrated dynamics wholes – ecosystems – is a science almost as old as civilization itself. The first description of an ecosystem has been attributed to Aristotle's disciple Theophrastus (371 - 288 BC), who synthesized the typical species composition and environmental conditions characteristic of mangroves. While the analysis of ecosystems and their underlying processes has been mainly framed in natural history since then, the rising concerns regarding human growing impact on nature prompted the emergence of a new field – ecology – more recently. The protection of ecosystems has been a core issue of ecology ever since, as we realized that our impact – through global warming of surface temperatures, habitat fragmentation and land-use change – threatened them, and the multitude of services they provide to human populations.

In this context of environmental crisis, biodiversity faces a major threat, as species are disappearing at an important and dramatically increasing rate across all major ecosystems. Some scientists are even mentioning a sixth mass extinction, thus putting on an equal footing the current extinction rates with those of the "big five" mass extinctions (respectively marking the end of the Ordovician, Devonian, Permian, Triassic and Cretaceous periods). Species extinction is not the only consequence of anthropogenic-driven global changes, their phenology and distribution are shifting and their comportment are changing. These processes all contribute to the emergence of novel communities, with changed composition and diversity of both species and their interactions. Understanding how these novel communities will sustain the functioning of ecosystems and the resulting ecosystem services is thus a pressing issue. In this context, investigating the reciprocal influence of ecosystems composition, structure and functions has emerged as a central problematic of ecology over the last decades.

"All have their worth and each contributes to the worth of the others."
— J.R.R. Tolkien, *The Silmarillion*

Chapter 1

Introduction

Hippos enjoying the morning sun in the mangroves of the Tana river delta, Kenya. Declared a wetland of international importance under the Ramsar Convention, these mangroves are home to a very diverse and tangled community, and to many people whose livelihood relies on its functioning. The construction of hydro-electric dams upstream, by disrupting the bi-annual flooding regime and the river flow threatens both the ecosystem community, its functioning and the livelihood of local populations.

1.1 The link between biodiversity and ecosystem functioning: a long-standing question

The intuition that biodiversity and the magnitude of ecosystem processes rates are correlated can be traced to the early 19th century, and what could be the first ecological experiment (Hector 2009). This experiment, performed by Sinclair (1816), described in fig 1.1, is what we could call today a biodiversity experiment, where species richness is experimentally manipulated and some measure of the assemblage functioning is recorded (here yield). The results of this experiment are later described first by Darwin & Wallace (1858) then by Darwin in his celebrated work *The Origin of Species* (Darwin 1859). He notes: "It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than in the former case."

A century later, Elton (1958) suggested that a decrease in biodiversity would affect negatively ecosystem functioning and stability, as it would decrease the number of interactions in the ecosystem and thus the number of alternative pathways for energy and nutrients. Along the same lines, using the concept of the ecological niche formalized by Hutchinson (1959), MacArthur (1970) hypothesized that communities with a rich resource base could maintain a more stable pool of consumers. These ideas led to a heated debate regarding the diversity-stability relationship (e.g., May 1972, 1974a; Pimm 1979). When looking at the data available today, one can easily observe that the global distribution of species diversity is indeed positively correlated to measures of ecosystem processes such as primary productivity. Fig. 1.2 shows for example how global tree species richness is correlated to productivity in forests (Liang et al. 2016). Explaining the fundamental mechanisms that explain the diversity-functioning relationship observable in ecosystems have been one of the central issues of ecology for a few decades now. The emergence of experimental ecology and the shift from observations in

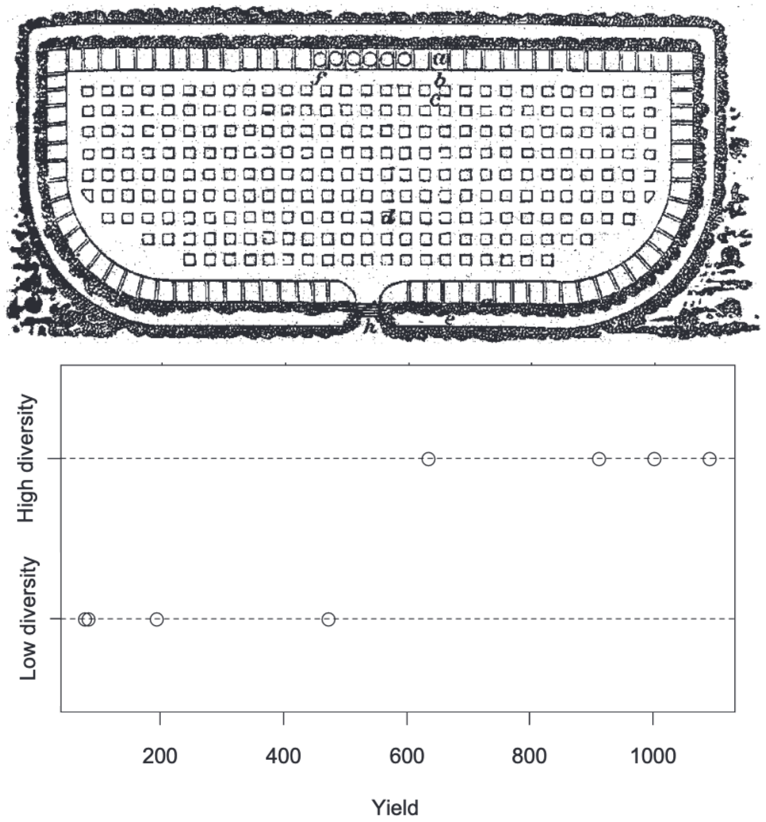


Figure 1.1 Figure adapted from Hector 2009. This figure describes what is probably the first ecological experiment, performed by Georges Sinclair, a Scottish horticulturist. The top panel describes the experimental settings, with plots (centre), beds (edges) and tanks for aquatic species (marked f). The data gathered through this experiment show a potential correlation between plant species richness and yield.

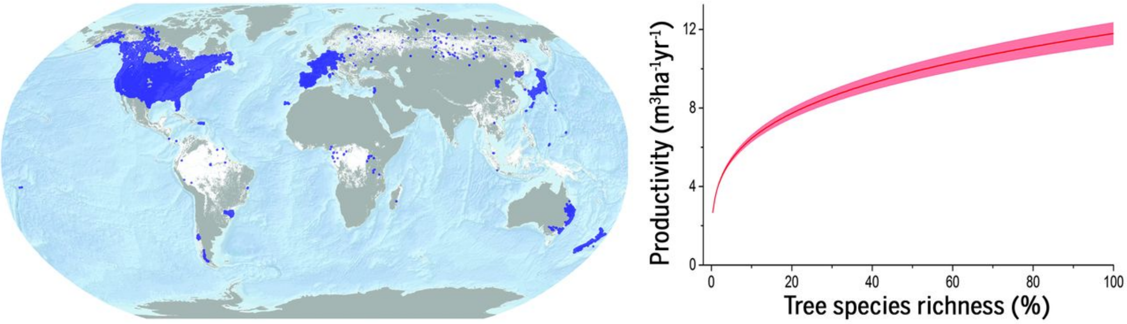


Figure 1.2 Figure from Liang et al., 2016. There is a positive asymptotic relationship between tree species richness and productivity (right) in global forests (shaded white on the map, green dots show the 777 126 sampled sites).

natural systems to the quantification of ecological processes has made possible to develop our understanding of these mechanisms that have been framed in what is now called the Biodiversity - Ecosystem Functioning (BEF) theory.

Before going into more details about the conceptual framework, it seems important to define fundamental concepts, notably biodiversity and functioning, which are central to this thesis.

Ecosystems are formed by a biotic community and its abiotic environment. All the organisms composing the ecosystem's community capture, mutualize and lose biomass as they grow, reproduce, live and die. In doing so they are embedded in a myriad of interactions of various nature with one another (competition, predation, pollination, etc.) and with their physical environment, and thus all dynamically contribute to shaping ecosystem processes and emerging properties. Ecosystem processes are the flows of nutrients and energy that are generated by the living organisms and their interactions with one another and with their environment (e.g., primary productivity, nutrient cycling, biomass flow between herbivores and carnivores, etc.). Ecosystem properties are the characteristics that result from these flows, such as producer biomass or number of persisting species. The term ecosystem functioning can refer to both (Hooper et al. 2005). In the context of this thesis, we focus on local communities, unaffected by environmental fluctuations and perturbations, and as such only study community functioning. I use this expression to refer to the rates at which biomass (a common currency used to represent nutrients and energy) is captured and transferred and the resulting stock of biomass in the different components.

Of all the interactions organisms can realize, shaping community functioning, trophic relationships are perhaps the most fundamental, as they are responsible for the transfer of nutrients and energy through the community (McCann 2012). Food webs, representing these feeding interactions (who eats whom) and mapping the resulting transfers of biomass, have then naturally been a frequently used representation of communities in ecology (Dunne 2006; McCann 2012). Following (Duffy et al. 2007), we can use two dimensions to describe food web species diversity. Horizontal diversity describes diversity within a focus trophic level, in which species display only competitive interactions. Vertical diversity conversely reflects the number of trophic levels, or food chain length. While many studies focus on either one of these dimensions, food webs are a useful tool to integrate both, as well as their interactions (as changes in horizontal diversity can alter vertical diversity and vice versa).

The term biodiversity (or diversity in the context of this thesis), while often used as a synonym of species richness, can encompass the variety of the living at a wide range of scales, from genetic diversity to groups diversity (Hooper et al. 2005), where groups are formed from the aggregation of organisms according to a shared characteristic of interest: functions, traits, niche, etc. Several metrics can also be used to quantify biodiversity from the simplest count of the number of entities to relative abundances, or presence-absence of focus entities (Hooper et al. 2005).

The emergence of the BEF field marks a paradigmatic shift in ecology. Biodiversity is not studied now only as a consequence of functioning, but also as a potential driver (Tilman et al. 2014). The results of these analyses, mainly obtained from experiments (Cardinale et al. 2007) show that the richest ecological communities also display the highest level of functioning up to a certain limit, whatever the metric used (e.g., carbon retention, standing biomass, primary production). This positive asymptotic relationship between diversity and functioning has since become a paradigm of ecology (Loreau 2010a; Tilman et al. 2014). However, the vast majority of these analyses focus on simple communities, where only competition for the shared resource affects species dynamics. It is difficult to measure the extent to which these results extend to real-world ecosystems.

At the same time, other domains of ecology also focus on investigating the factors driving community functioning. This is notably the case of food chain ecology, which – since its foundation by Elton (1927) – investigates the consequences of consumption on the transfer of matter and energy in trophic chains (Lindeman 1942; Oksanen et al. 1981; Fretwell 1987; Wilkinson & Sherratt 2016). Although these fields (BEF and food chain analysis) deal with closely related issues - the functioning of communities, the use of different methods and concepts creates a theoretical divide that prevents our understanding of functioning in natural complex systems. It will thus not be long after the first BEF results before some authors realize that to really understand - and ultimately predict - the functioning of communities, it is necessary to bridge this theoretical divide by including the different concepts linked to both competition and consumption in a single framework (Duffy et al. 2007).

Food webs present a natural framework for this reconciliation as they integrate both dimensions of diversity mentioned above. On the one hand, they represent the diversity of species within the same trophic level, competing for the same resources and avoiding the same set of consumers (often referred to as horizontal diversity; Duffy et al. 2007; Loreau 2010a) and on the other hand, they also represent the vertical aspect of diversity, i.e., food chain length (Duffy et al. 2007; Loreau 2010a; Wang & Brose 2017). Food webs also represent in detail all trophic interactions within a community thus providing an explicit map of the biomass fluxes between species (Pascual & Dunne 2006). Coupled with adapted resource-consumer models, food webs thus offer an ideal framework for reconciling concepts from BEF theory with those from food chain theory (Martinez et al. 2006). Initial work using this framework to test the validity of BEF theory in complex communities has shown that the effect of diversity seems to be strongly dependent on the organization of interactions within it, i.e., its structure (Thébault & Loreau 2003; Loreau 2010a). Analysis of the structure of food webs – using methods adapted from graph theory – then becomes a new necessity to continue this effort to understand the link between diversity and functioning in natural ecological communities.

The work presented here aims at building and testing a methodological framework to answer the following question: **how does the structure of food webs influence the diversity-functioning relationship in complex ecological communities?** In this introduction, I will start by giving a more detailed overview of the conceptual background presented above, from analyses of food chains functioning and diversity experiments to the more recent analysis of complex systems by the means of graph theory. By laying out the concepts and results, stemming from each of the conceptual frameworks presented, that have been identified as important in our understanding and predictions of community functions, the literature review below outlines a set of ecological processes that are fundamental in understanding the link between diversity and functions. I then identify a methodological framework that integrates all of these processes — hereafter called **ingredients** — which will allow us to synthesize our knowledge and move towards more accurate predictions of community functioning. I will then explain how my research builds on that conceptual background and methodological framework to advance our knowledge of the diversity-functioning relationship in complex ecological communities.

1.2 Conceptual background: insights on community functioning from diverging domains of ecology

1.2.1 A food chain perspective: consumption shapes community structure

Food chains present a simple way of representing ecological communities (Elton 1927; Lindeman 1942; Fretwell 1987). They are built on the assumption that species that share a similar set of resources and consumers — thus at a similar trophic level — share similar properties and constraints. Since i) the majority of species have discrete trophic levels (Williams & Martinez 2004), ii) trophic level and body size are often correlated and iii) body size and biological rates are also correlated, this representation is particularly practical and presents a certain degree of realism. The study of trophic chains has led to major advances in both ecosystem and community ecology, and has been key in studying the effect of consumption and the subsequent movement of matter and energy on the functioning of trophic compartments or the system as a whole (Fretwell 1987).

The food chain approach has also helped uncovering the mechanisms that govern and constrain the transfer of matter between compartments. This allowed to understand, among other things, the origin of a global phenomenon: the emergence of bottom-heavy biomass pyramids and the conditions applying in the communities that deviate from them (Wang et al. 2009; Trebilco et al. 2016; Woodson et al. 2018). What is often referred to as the Eltonian pyramid (Elton 1927) initially describes a decrease in the abundance of individuals as we move up the food chain (Jonsson et al. 2005; Begon et al. 2006), but the concept applies equally to biomass (Bodenheimer 1938; Lindeman 1942) and energy transfers between compartments (Lindeman 1942; Hatton et al. 2015; Trebilco et al. 2016). The mechanisms known to cause this phenomenon are metabolic losses and imperfect assimilation during the consumption process. Numerous studies are investigating how body size distribution, the resulting allometric scaling of biological rates and environmental factors influence these mechanisms (McCauley et al. 2018;

Woodson et al. 2018). These studies have contributed greatly to our knowledge regarding the distribution of biomass in the food chain in various conditions (Dortch & Packard 1989; Tunney et al. 2012; McCauley et al. 2018), the allometric scaling of biological levels (Hatton et al. 2015; Trebilco et al. 2016) and the scaling between different measures of functioning (Hatton et al. 2015). This shows us **the key role of certain traits (especially metabolic class and body size) in constraining energy and matter transfers in communities, because of the allometric scaling of biological rates (ingredient 1).** Note that by metabolic classes (or categories) we mean whether the species is a producer, an invertebrate or a vertebrate. Species from different metabolic classes have very different metabolisms (and as such different allometric coefficients).

A more dynamic view of similar problems – i.e., the link between consumption mechanisms and the generalities observed in ecological communities – has also been used. The development since Lotka (Lotka & Lotka 1956) and Volterra (Volterra 1928) of resource-consumer models has been the origin of a central concept of ecology: the trophic cascade (Hairston et al. 1960; Paine 1980; Fretwell 1987). The concept of trophic cascade describes how changes in one level of the food chain can have cascading consequences on all other trophic levels through top-down (Hairston et al. 1960) or bottom-up (Ohgushi & Sawada 1985; Power 1992) trophic control. Community-level cascades (Polis 1999) informs us about the cascading consequences of manipulating the vertical component of diversity. As an example, the addition of an extra trophic level — e.g., invasion or large increase in the abundance of a top predator — is known to have an alternating effect on the different levels of the trophic chain that it dominates (Estes & Palmisano 1974). The potency of herbivores is also known to have large consequences on the productivity of a community (Carpenter & Kitchell 1988; Polis 1999). A classic example is the sea otter, urchin and kelp forest system in the Aleutian Islands (Estes & Palmisano 1974; Estes et al. 1998), near-extinction of otters due to either over-hunting by humans or predation by killer whales can lead to the deforestation of kelp forests through the release of urchins that graze on kelp. Besides the analysis of the effect of trophic chain length on the density and functioning rates of the different compartments, the concept of trophic cascade is used to investigate various other questions concerning the relative strength of top-down or bottom-up mechanisms (Borer et al. 2005) according to different factors such as ecosystem types (Strong 1992; Schmitz et al. 2000; Halaj & Wise 2001; Shurin et al. 2002) or environmental variations (Leibold 1989). The corpus of results that has emerged gives us a fairly detailed picture of the factors that govern biomass dynamics, constrained by trophic control, in resource-consumer systems. If we want to understand the functioning of complex ecological communities, facing changes in diversity, **including the possibility for trophic control is necessary, highlighting the importance to frame our analyses of functioning in adapted dynamic consumer-resource models (ingredient 2).**

Another important insight from the dynamic analysis of food chains is the effect of omnivory on trophic control. As Polis & Strong (1996) put it, "[. . .] much theory relies on the idealization of 'trophic levels' connected in a single linear chain." However, more complex interactions such as omnivory and intraguild predation (IGP) are widespread in real-world communities. Analysis of their abundance in empirical systems first led to believe that most species occupy integer trophic positions (Williams & Martinez 2004) but, later analysis showed that – while that is true – many of the species that do occupy these integers trophic positions are producers and herbivores, making the secondary consumer compartment a "tangled web of omnivores" (Thompson et al. 2007). The effect of omnivory and IGP on community stability and the predictability of the effect of trophic cascades are the subject of many experiments. The role of omnivory is still unclear, and while it does not necessarily preclude the occurrence of trophic cascades (Okun et al. 2008), its action on different trophic levels makes its consequences often unpredictable (Pimm & Lawton 1978; Holt & Polis 1997; Mylius et al. 2001; Vanni et al. 2005), especially as its effect on stability seems to depend on primary production (Holt & Polis 1997; Mylius et al. 2001). These results show us that if we are to simulate realistically the functioning of ecological communities, we need to use a methodological framework that **includes complex interactions such as omnivory and IGP and allows the precise estimation of their consequences (ingredient 3).**

1.2.2 Zooming in on food chain compartments: competitive interactions shape the BEF relationship in horizontal communities

First explicit explorations of the influence of biodiversity on ecosystems properties and processes occurred almost three decades ago, motivated by the growing realization that the human-driven biodiversity erosion could result in altered ecosystems services (Schulze & Mooney 2012). Although a few considered a multi-trophic system (e.g., Naeem et al. 1994) defined as a food web with several levels, the majority studied the impact of horizontal species diversity - the diversity occurring within a single level, mostly primary producers - on several indicators of communityfunctioning such as standing biomass, productivity, nutrient and water retention and stability (Hooper et al. 2005; Loreau 2010b). These experiments usually consisted in manipulation of plant species richness and composition (e.g., the seminal work of Tilman & Downing 1994). They showed that, in this context, when species richness increases, community functions such as standing biomass, primary production, resistance to drought, nutrient retention and community stability increased as well (Tilman & Downing 1994; Tilman et al. 1996). These results were reproduced across different types of ecosystems and trophic levels and produced strong evidences of a positive and asymptotic BEF relationship, consistent across many experiments for several indicators of functioning and independent of trophic levels and study systems (Cardinale et al. 2012; Griffin et al. 2013).

Although experiments and observations showed a general response of several indicators of functioning to diversity, they also generated years of debate regarding the underlying mechanisms and the relative importance of identity and richness (Aarssen 1997; Tilman 1997a; Huston et al. 2000; O'Connor & Crowe 2005), which resulted in the development of a conceptual framework for BEF studies (Loreau & Hector 2001; Loreau 2010a). The consensus now is that the positive BEF relationship emerges from the simultaneous effect of two main classes of mechanisms, the selection effect (Tilman 1997b; Loreau & Hector 2001) and the complementarity effect (Tilman 1997b; Loreau 2000; Loreau & Hector 2001). The selection effect is a generalization of the sampling effect based on the assumptions that i) a highly effective species is more likely to be present in more diverse communities and ii) the strongest competitor is also often the most effective species and will eventually come to dominate the mixture. Traits variation is an initial condition and a selective process then promotes dominance by species with particular functional traits that affect species' competitive abilities (Loreau & Hector 2001). The complementarity effect is based on the assumption that high diversity provides more functional traits variation and is attributed to niche partitioning (Northfield et al. 2010) and facilitation (Loreau 2010b). Although these two classes of mechanisms have a joint action, functional complementarity is predominant and tends to increase over time (Cardinale et al. 2007). In the same study, selection has been found to be often only important in the early stage of a community (Cardinale et al. 2007). This counter-intuitive result (pioneer species are usually opportunistic, poorly competitive species) shows the potential difficulty to map results from experiments to real-world systems. In experiments, plots are usually seeded at high density, artificially increasing the importance of competitive abilities in the early stages. Similarly, the type of function we chose to focus on (biomass storage and nutrient retention) may cause artificial correlation between diversity and functions, because they are highly correlated to competitive abilities (Winfree 2020). In real-world ecosystems, where species have to face environmental fluctuations and external perturbations, other functions may be more important, and less correlated to competitive abilities (Winfree 2020). Moreover, because early BEF studies focused mostly on grasslands, the fundamental mechanisms only integrated interaction occurring between the organisms within a single level: competitive interactions (Hines et al. 2015) to the detriment of other types of interactions.

Given the importance of competition on shaping the functioning of trophic compartments, the ideal methodological framework for analyzing ecological communities functioning must include the possibility for **competition between species (ingredient 4)**, across and within compartments. Between heterotrophs, competition emerges from trophic interactions, when two consumers share the same resource (exploitative competition) or when two resources have the same consumers (apparent competition). But competition between autotrophs must also be accounted for, at the basal level of the community, as their productivity sustain the whole system.

1.2.3 Trophic cascade alters the effect of biodiversity on ecosystem functioning

While BEF theory tells us that within a trophic level, through mechanisms rooted in competition, biodiversity begets higher levels of functioning (section 1.2.2), food chain theory suggests that consumption could potentially alter the strength of competition within a trophic level (section 1.2.1). This is a strong argument for the integration of both the vertical and horizontal dimensions of diversity in analyses of community functioning. Many studies – reviewed by Duffy et al. (2007) – analyzed the effect of trophic interactions on the BEF relationship at one focus level. These studies focused mainly on how variations in diversity at one trophic level change the diversity-functioning relationship at other trophic levels, and the effect of food chain length on these cascading effects (Schmitz et al. 2000; Thébault & Loreau 2003; Downing & Wootton 2005; Duffy et al. 2005; Holt & Loreau 2013). The effect of plant species richness on primary productivity for instance depends on the diversity of herbivores and the number of trophic levels (food chain length; Duffy et al. 2007). These results, beyond their intrinsic relevance, show the importance of considering the interplay between processes that emerge from consumption and competition. But the study systems used are often simplified communities, with only few species and discrete trophic levels.

This disconnection between vertical and horizontal diversity in BEF studies is not representative of the overall biodiversity and therefore prevents a global understanding of BEF relationship (Thébault & Loreau 2006; Duffy et al. 2007; Loreau 2010b; Thompson et al. 2012). Ecosystems are not only an assemblage of species but also underlain by a set of interactions that form an integrated system often described as a "tangled bank." Trophic interactions are not only direct paths from producers to top predators, and while it is true that many species have a discrete trophic level, interactions such as omnivory, intraguild predation, or processes such as ontogenetic diet shifts are blurring the frontiers between "levels", and these interactions are known to have important dynamic effects. Therefore, the need for the integration of species and interactions diversity has been widely acknowledged (Duffy 2003; Thébault & Loreau 2003; Duffy et al. 2007). Food webs map the energy and nutrient fluxes within the species diversity of an ecosystem. They provide a natural framework to study the mechanisms of the BEF relationship (Thompson et al. 2012), and incorporate concepts from both food chain and BEF theory, while also investigating the potential effect of the structure of interactions (Barbier & Loreau 2019). An explicit food web perspective is the natural next step in improving our understanding of BEF relationship (Thébault & Loreau 2006; Duffy et al. 2007; Rooney & McCann 2012; Thompson et al. 2012; Poisot et al. 2013; Hines et al. 2015).

1.3 Food webs as a natural framework for synthesis

Food webs describe the trophic interactions between organisms in a community, they can be visualized using graphs, where nodes are often populations and edges are the directed trophic interactions between them. May (1972); May (1974a) applied a simple consumer-resource model to random food webs and showed that in this context, there is no apparent mathematical reason why our observation that richer ecosystems appear to be more stable should be true. Conversely, he showed that species-rich networks often have chaotic dynamics. This spurred the search for the hidden mechanisms responsible for ecosystem stability. As random food webs were unstable, identifying how structure drives community dynamic processes became a main research hypothesis. The "diversity-stability" debate that ensued produced much of what we know today about the link between a community topological and dynamic properties.

Food webs are surprisingly similar in their topology (Cohen et al. 1990; Dunne et al. 2002a; Jordano et al. 2003; Bascompte & Melián 2005; Pascual & Dunne 2005; Stouffer et al. 2005, 2006), regardless of the identity of the species involved or ecosystem types, revealing that some dynamic and evolutionary constraints are at play in shaping them. Many food web properties (e.g., intervality and connectance), that estimate various ecological processes (e.g., foraging and allometric rules and proportion of specialists), display striking generalities (Pascual & Dunne 2006). The existence of these generalities in the organization of trophic interactions across ecosystems suggests that the paths of matter and energy allocations are constrained by the mechanisms that cause the potential realization of such interactions. If food webs evolved allowing the transfer of energy from primary producers to top predators, their structure is likely to play an important role in functioning.

Milo (2002) showed for example that different types of networks (neural, electrical, ecological, etc.) have a characteristic motif distribution. Motifs are all the different subwebs of 3 nodes (species in the context of food webs) contained in a network. They are particularly interesting because they represent the basic "building blocks" of networks. Among different types of networks, food webs are characterized by an over-representation of the motifs $A \rightarrow B \rightarrow C$ (linear chain; arrows go from consumer to resource) and $A \rightarrow B \rightarrow C \leftarrow A$ (omnivory or intraguild predation) and an under-representation of the motifs $A \rightarrow B \leftarrow C$ (exploitative competition) and $A \leftarrow B \rightarrow C$ (apparent competition), relatively to random networks (Bascompte & Melián 2005; Camacho et al. 2007; Stouffer et al. 2007). This invariant in the structure of food webs carries an important information as these motifs represent the basic modules between species (respectively a linear food chain, omnivory, apparent and exploitative competition) and as the dynamics of these modules (Holt 1997b) have been extensively studied. Omnivory motifs in particular (and intraguild predation) and their contribution to food web dynamics have been extensively studied. While early work by Pimm & Lawton (1978) showed that omnivory could potentially have a destabilizing role (using a Lotka and Volterra type model; Lotka & Lotka 1956; Volterra 1928), the ubiquity of omnivory (defined as the presence of species feeding on more than one trophic level) in natural food webs made ecologists question that result. It was later found, using a more realistic model but simplified food webs (more precisely a Rosenzweig 1973 dynamic model; with biological rates parameterized using allometric relationships following Yodzis & Innes 1992) that omnivory may have a stabilizing role (McCann & Hastings 1997). The role of omnivory in complex food webs stayed unclear until explored in the light of interaction strength.

Using more realistic models of biomass transfer – that integrate allometrically scaled biological rates – to investigate the link between topology and dynamics allowed to shed new light on the link between food webs structure and dynamics. An important contribution of this type of model was the possibility of analyzing structure in light of interaction strength (in the context of food webs, we usually quantify interaction strength using biomass flow). Having this type of weighed structural analysis made it possible to gather more evidence of the role of omnivory for example. It appears that while strong omnivory links destabilize structure, weak links (that appear to be more frequent) can stabilize community dynamics (Gellner & McCann 2012, 2016; Wootton 2017). Actually, in food webs, the rule seems to be “many weak links and a few strong”, with weak links stabilizing community dynamics by dampening oscillations and as such reducing species probability of extinction (McCann et al. 1998). In the context of food webs, interaction strength can be related to the turnover rate of biomass (production:biomass ratio). This concept has been used to show that empirical food webs seem to be compartmentalized into biomass channels (Rooney et al. 2006). In natural systems, biomass comes from nutrient compartments (e.g., detritus, fungi, phytoplankton). A channel is defined as a compartment into which species get the bulk (more than an arbitrary threshold) of their biomass from one of these compartments. Channels appear to be asymmetrical in empirical systems (e.g., one has stronger links, which can be modelled by higher attack rates) creating an asynchrony in biomass dynamics. Higher-level consumers then couple the different channels. This asynchrony makes systems more stable, particularly by providing a more stable prey base for consumers that are thus less threatened by extinction (Rooney et al. 2006). This type of result shows the importance of integrating structural analyses of food webs into dynamic models able to account for realistic mechanisms of biomass transfers to understand the emergence of community functions.

1.4 The bioenergetic food-web model

To synthesize the results of the different approaches mentioned so far, we need a methodological framework that would allow us to integrate the four ingredients mentioned above:

1. realistic energy and matter transfers, through trophic interactions, based on the allometric scaling of biological rates;
2. the inclusion of these transfers in a dynamic consumer-resource model;
3. the adaptation of this model to food webs, where species can have multiple resources and/or consumers;
4. the inclusion of competition between basal heterotroph species.

Such a framework makes it possible to integrate the dynamic consequences of consumption, the influence of the food web structure of the communities, allometric scaling and the effect of competition between basal species (the producers) as well as competition emerging from trophic interactions (when species share similar resources or consumers). In turn this would allow us to test the interplay between the structure of food webs and the mechanisms emerging from competition and consumption respectively.

The bioenergetic model for food webs, with the addition of a nutrient-intake model for producers growth, offers such a framework. This consumer-resource model was originally developed by Yodzis & Innes (1992) and immediately led to important advances in ecology

(Williams et al. 2007). More recently, it has been adapted for use in food webs through the implementation of a multi-species functional response (Williams et al. 2007). The particularity of this model, that made its success, is that the biological rates (for consumption, metabolism and growth of basal species) vary according to the body masses of the species participating in the interaction and their metabolic classes. The allometric coefficients and exponents are based on empirical data, giving the model a degree of grounding in reality that others often do not have (Williams et al. 2007). Body size is often referred to as a super-trait because it is, on the one hand, easy to measure and, on the other hand, it scales with many physiological processes (Whitfield 2004). This model therefore offers a balance between simplicity - a tractable number of parameters - and realism (Williams et al. 2007). Including a nutrient intake model for producers growth (Tilman 1982; Huisman & Weissing 1999; Brose et al. 2005b, 2005a; Brose 2008) allows including explicitly competition at the basal level, and to quantify the intake of the community, through heterotrophs.

The adaptation of this model to the simulation of biomass dynamics in food webs is at the origin of recent results testing the existence of the BEF relationship in complex ecological communities, and the potential mechanisms that govern it (Schneider et al. 2016; Wang & Brose 2017; Wang et al. 2019). In early BEF studies in which the underlying structure of trophic interactions has been provided, BEF relationships appear to be more diverse than the monotonic changes predicted within a single trophic level (Thébault & Loreau 2003; Thébault et al. 2007) which suggests a strong dependence of the BEF relationship on food web structure. However, more recently, Schneider et al. (2016) has shown that a positive and asymptotic relationship seems to exist between animal richness and biomass fluxes and stocks in food webs. Other propose that the height of the trophic chain (the vertical diversity of the community) is at the origin of a selection of particularly productive basal species, at the origin of the BEF relationship in food webs (Wang & Brose 2017). They also show the importance of intra-guild predation in the emergence of the BEF relationship (Wang et al. 2019). This same model has led to other major advances in recent years, such as the recognition of the importance of allometric scaling for trophic network stability and community persistence (Brose et al. 2006b; Brose 2008). While other models have been used to investigate the mechanisms underlying BEF relationships in food webs (Poisot et al. 2013 for example), their predictions and the processes they arise from could be easily integrated within the bioenergetic food-web model. This model, which makes including all the concepts that interest us possible – while still being tractable – therefore offers an ideal candidate to be a common platform for synthesis.

1.5 Main questions and objectives

Based on the conceptual framework detailed above we see that while being able to predict the functioning of novel communities (with changed composition and structure) is always at the heart of our concerns, relatively few studies look at the influence of the structure of food webs, and no consensus has yet emerged about the effect of diversity in complex ecological communities. I argue here that to understand the joint effect of structure and diversity on the functioning of food webs, it is necessary to develop and synthesize the different results that have emerged from both food chain, BEF and food web analysis approaches in an adapted framework. To do so, we need

- a common methodological framework integrating the four ingredients outlined above which would allow us to integrate and compare the conditions for the emergence of the predictions from the different approach and understand how they fit together;
- to understand the effect of food-web structure on these results, which requires finding suitable measures of structure.

Chapters 2 and 3 of this thesis focus on implementing and assessing the tools needed, and chapter 4 builds on these tools to analyze the effect of food-web structure on the emergence of the various predictions mentioned, namely the effect of food chain length, complex trophic interactions, allometric scaling and the BEF positive relationship.

The **second chapter** of this thesis describes the implementation in a common and efficient platform of the bioenergetic food-web model: `BioEnergeticFoodWeb.jl` . This model has been recognized as ideal for integrating the different mechanisms of competition and consumption, and the relationship between the two, and thus offers a natural candidate as a common tool for synthesis. This is a somewhat unusual chapter since the `BioEnergeticFoodWeb.jl` package is still under development and now has many new features and improvements since compared to the time of publication. Most of these changes were born from new collaborations with scientists interested in our platform and working on various thematics, showing, we hope, the successful takeoff of this new common platform and its potential for synthesis. These changes are described in the discussion that closes this thesis.

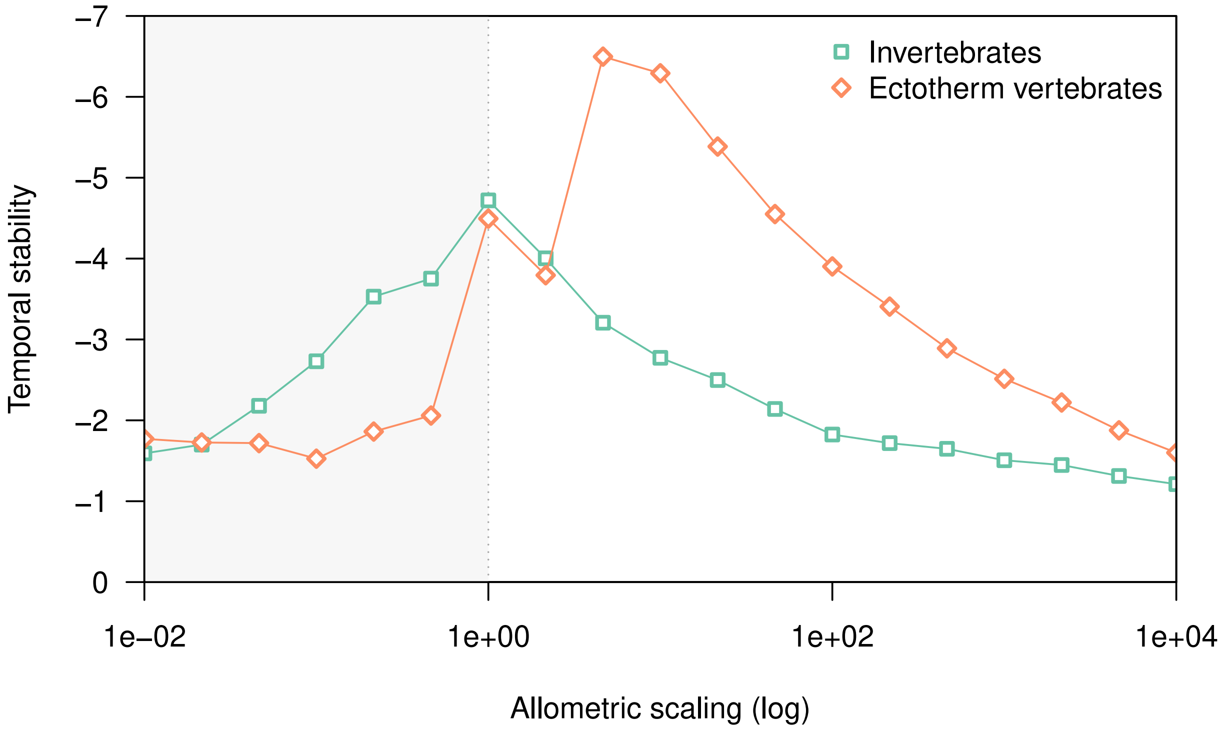
The BEFWm, and its implementation in the high-performance language `Julia` , give us an efficient way to simulate the functioning of food webs, and the ability to test the influence of the structure on the functioning. However, while there are a variety of ways to measure food-web structure, we also need to understand what these metrics tell us about the ecological processes they are supposed to represent, and how they can also be influenced by other factors or simply emerge from mathematical constraints.

The **third chapter** of this thesis addresses these questions. This chapter is a critical review of the different methods of food web analysis. By critical I mean that this review is not meant to be exhaustive but rather an assessment of the methodological development of a core set of methods that are robust and informative, the questions they can address, and their limitations. Building this review collaboratively with many experts in the field also allowed me to select strategically the structural measures used for the fourth chapter, and to assess their ecological grounding.

Finally, the **fourth chapter** assesses the ability of the bioenergetic model to reproduce the various predictions mentioned above and serve as a framework for synthesis. Through the joint use of concepts developed through food chains, food webs and BEF analyses, we show the links between these different concepts by analyzing the interplay between their predictions. Specifically we show that while the majority of communities are bottom heavy (meaning that most of the community biomass is stored in primary producers at the basal level of the food web), coherently with what we observe in natural systems (a “green world”), rarely top-heavy communities can persist in the absence of subsidies. These communities seem to display a particular food-web structure, relatively more complex (densely connected and with higher levels of omnivory or IGP) and with a higher consumers-resource body-mass ratio. This structure is correlated to more important fluxes between compartments and a higher efficiency to store the biomass produced, which in turns allows the persistence of a heavy consumer compartment. The results of this chapter, by highlighting these links between trophic network structure, biomass distribution and diversity-functioning relationships, shed new light on the predictions of functioning in the complex ecological community and the future developments that are needed.

Chapter 2

Biomass dynamics in community food webs



Biomass dynamics in community food webs

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Summary

1. Food webs are the backbone upon which biomass flows through ecosystems. Dynamic models of biomass can reveal how the structure of food webs is involved in many key ecosystem properties, such as persistence and stability.
2. In this contribution, we present BioEnergeticFoodWebs, an implementation of Yodzis & Innes (The American Naturalist 139, 1151?1175, 1992) bio-energetic model, in the high-performance computing language Julia.
3. We illustrate how this package can be used to conduct numerical experiments in a reproducible and standard way.
4. A reference implementation of this widely used model will ease reproducibility and comparison of results across studies.

2.1 Introduction

Community and ecosystem ecologists have long sought to understand the diversity, properties and dynamics of multi-species assemblages. The characteristics of communities emerge in unpredictable ways because species influence one another through direct, and indirect, ecological interactions. Seeing that the coexistence of populations is constrained at least by feeding interactions, models of the relationship between resources and consumers have provided a useful and frequent tool in studying the theory of community dynamics. Although these modelling efforts started from simple, abstract models like those from the Lotka-Volterra family (Bacaër 2011), more tailored and parameterized models have emerged whose goal was to include a broader range of ecological and biological mechanisms, thus hopefully providing more realistic representations of empirical systems. Among these, the "bio-energetic" model of Yodzis & Innes (1992) is a general representation of resource-consumer dynamics, yielding results comparable to empirical systems, while needing minimal parameters. This trade-off between minimal complexity (we only need to provide species metabolic type and typical body size, two easy-to-measure parameters) and maximum ecological realism allows scaling up from modelling simple few-species and few-interaction systems to more realistic species-rich, dense communities.To achieve this purpose, it uses allometric scaling of metabolic biomass production and feeding rates, meaning that the flow of biomass from a resource to its consumer is based on realistic energetic constraints.

While the model developed by Yodzis & Innes (1992) provides a useful tool to study pairwise interactions, we know that the dynamics of ecological communities are driven by the entanglement of these interactions in larger networks (Camerano 1880; May 1972; Chesson & Kuang 2008). We also know that disturbances affecting species biomass or density cascade up, not only to the species that they interact with but also with species up to two degrees of separation from the original perturbation (Berlow et al. 2004). In this context, models of energy transfer through trophic interactions are better justified when they account for the entire food-web structure, such as Williams et al. (2007) adaptation of Yodzis & Innes (1992) model. This food-web bio-energetic model has been used, for example, to show how food web stability can emerge from allometric scaling (Brose et al. 2006b) or allometry-constrained degree distributions (Otto et al. 2007) (more past uses of the model are described in supplementary table S2.1). Yet, although these and other studies used the same mathematical model, implementations differ from study to study and few have been released. Motivated by the fact that this model addresses mechanisms that are fundamental to our understanding of energy flow throughout food webs, we present `BioEnergeticFoodWebs.jl` , a *Julia* package implementing Yodzis & Innes (1992) bio-energetic model adapted for food webs (Williams et al. 2007) with updated allometric coefficients (Brown et al. 2004; Brose et al. 2006b).

This package aims to offer an efficient common ground for modelling food-web dynamics, to make investigations of this model easier, and to facilitate reproducibility and transparency of modelling efforts. Taking a broader perspective, we argue that providing the community with reference implementations of common models is an important task. First, implementing complex models can be a difficult task, in which programming mistakes will bias the output of the simulations, and therefore the ecological interpretations we draw from them. Second, reference implementations facilitate the comparison of studies. Currently, comparing studies means not only comparing results but also comparing implementations – because not all code is public, a difference in results cannot be properly explained as an error in either study, and this eventually generates more uncertainty than it does answers. Finally, having a reference implementation eases reproducibility substantially. Specifically, it becomes enough to specify which version of the package was used, and to publish the script used to run the simulations (as we do in this manuscript). We fervently believe that more effort should be invested in providing the community with reference implementations of the models that represents cornerstones of our ecological understanding.

2.2 The model

2.2.1 Biomass dynamics

We implement the model as described by Brose et al. (2006b), which is itself explained in greater detail in Williams et al. (2007). This model describes the flows of biomass across trophic levels, primarily defined by body size. It distinguishes populations based on two variables known to drive many biological rates: body mass (how large an organism is, *i.e.* how much biomass it stocks) and metabolic type (where the organism get its biomass from and how it is metabolized). Once this distinction made, it models populations as simple stocks of biomass growing and shrinking through consumer-resource interactions. The governing equations below describe the changes in relative density of producers and consumers respectively.

$$B_i' = r_i G_i B_i - \sum_{j \in \text{consumers}} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{2.1}$$

$$B_i' = -x_i B_i + \sum_{j \in \text{resources}} x_i y_i B_i F_{ij} - \sum_{j \in \text{consumers}} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{2.2}$$

where B_i is the biomass of population i, r_i is the mass-specific maximum growth rate, G_i is the net growth rate, x_i is i's mass-specific metabolic rate, y_i is i's maximum consumption rate relative to its metabolic rate, e_{ij} is i's assimilation efficiency when consuming population j – which represent the proportion ($e_{ij} \in [0, 1]$) of biomass lost by j that is assimilated by i– and F_{ij} is the multi-resources functional response of i consuming j:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c_i B_i B_0^h + \sum_{k=resources} \omega_{ik} B_k^h} \tag{2.3}$$

2.2.2 Growth rate function

The formulation of the growth rate G_i can be chosen among three possibilities (Williams 2008) that all share the general equation of $G_i = 1 - s/k$, where s is the sum of biomass of populations in competition for a resource with carrying capacity k. The first scenario, used by Brose et al. (2006b), sets $s = B_i$ and $k = K$: species only compete with themselves for independent resources. The issue with this formulation (Kondoh 2003) is that the biomass and productivity of the system scales linearly with the number of primary producers. The second formulation "shares" the resource across primary producers, with $s = B_i$ and $k = K/n_P$, wherein n_p is the number of primary producers. Finally, a more general solution that encompasses both of the previous functions is $s = \sum \alpha_{ij} B_j$, with α_{ii} (intraspecific competition) set to unity and α_{ij} (interspecific competition) taking values greater than or equal to 0. Note that $\alpha_{ij} = 0$ is equivalent to the first scenario of $k = K$ and $s = B_i$.

2.2.3 Numerical response

In equation 2.3, ω_{ij} is i's relative consumption rate when consuming j, or the relative preference of consumer i for j (McCann et al. 1998; Chesson & Kuang 2008). We have chosen to implement its simplest formulation: $\omega_{ij} = 1/n_i$, where n_i is the number of resources of consumer j. The Hill coefficient h is responsible for the hyperbolic or sigmoidal shape of the functional response (Real 1977), B_0 is the half-saturation density and c quantifies the strength of the intraspecific predator interference – the degree to which increasing the predator population's biomass negatively affect its feeding rates (Beddington 1975; DeAngelis et al. 1975). Depending on the parameters h and c the functional response can take several forms such as type II ($h = 1$ and $c = 0$), type III ($h > 1$ and $c = 0$), or predator interference ($h = 1$ and $c > 0$).

2.2.4 Metabolic types and scaling

As almost all organisms' metabolic characteristics vary predictably with body mass (Brown et al. 2004), these variations can be described by allometric relationships as described in Brose et al. (2006b). Hence, the per unit biomass biological rates of production (R), metabolism (X)and maximum consumption (Y)follow negative power-law relationships with the typical adult body mass (M)(Savage et al. 2004; Price et al. 2012).

$$R_P = a_r M_P^{-0.25} \tag{2.4}$$

$$X_C = a_x M_C^{-0.25} \tag{2.5}$$

$$Y_C = a_y M_P^{-0.25} \tag{2.6}$$

where the subscripts P and C refer to producers and consumers populations respectively, M is the typical adult body mass, and a_r, a_x and a_y are the allometric constant. To resolve the dynamics of the system, it is necessary to define a timescale. To do so, these biological rates are normalized by the growth rate of a chosen (usually the smallest) producer population (*cf.*

eq. 2.4) (Brose et al. 2006b; Williams et al. 2007).

$$r_i = \frac{a_r M_P^{-0.25}}{a_r M_P^{-0.25}} = 1 \tag{2.7}$$

$$x_i = \frac{a_x M_C^{-0.25}}{a_r M_P^{-0.25}} = \frac{a_x}{a_r}(\frac{M_C}{M_P})^{-0.25} \tag{2.8}$$

In equations eq. 2.1 and 2.2, y_i refer to the maximum consumption rate of population i relative to its metabolic rate and thus become a non-dimensional rate:

$$y_i = \frac{Y_C}{X_C} = \frac{\frac{a_y M_P^{-0.25}}{a_r M_P^{-0.25}}}{\frac{a_x M_C^{-0.25}}{a_r M_P^{-0.25}}} = \frac{a_y}{a_x} \tag{2.9}$$

As the biological rates also vary with the organisms metabolic types, the maximum consumption rate of population i relative to its metabolic rate (y_i) is not the same for ectotherm vertebrates ($y_i = 4$) and invertebrates ($y_i = 8$) predators, the same goes for the allometric constant a_x, which causes the mass-specific metabolic rate (x_i) to differ for ectotherm vertebrates ($a_x = 0.88$) and invertebrates ($a_x = 0.314$). The diet of predators also affects their assimilation efficiency (e_{ij}) which is greater for carnivores ($e_{ij} = 0.85$) than for herbivores ($e_{ij} = 0.45$).

Based on the observation that most natural food webs have a constant size structure (Brose et al. 2006a; Hatton et al. 2015), the consumer-resource body-mass ratio (Z) is assumed to be constant. The body mass of consumers is then a function of their mean trophic level (T), it increases with trophic levels when $Z \geq 1$ and decreases when $Z \leq 1$:

$$M_C = Z^{T-1} \tag{2.10}$$

where M_C is the body mass of consumers, normalized by the body mass of the basal species ($T = 1$) to make the results independent of the body mass of the basal species. When simulating empirical food webs, it is also possible to provide a vector of the sampled average body masses.

2.2.5 Setting the simulation parameters

All of these parameters can be modified before running the simulations (see `?model_parameters`), and are saved alongside the simulation output for future analyses. The default values and meanings of the different parameters are explained in the documentation of the `model_parameters` function. The user can specify which species are ectotherm vertebrates by supplying an array of boolean values, and the body mass of each species by supplying an array of floating-point values.

2.2.6 Saving simulations and output format

The core function `simulate` performs the main simulation loop. It takes two arguments, `p` – the dictionary generated through the `model_parameters` function and containing the entire set of parameters – and `biomass` , a vector that contains the initial biomasses for every population. Three keywords arguments can be used to define the initial (`start`) and final (`stop`) times as well as the integration method (`use` , see `?simulate` or the on-line documentation for more details on the numerical integration methods available). This function returns an object with a fixed format, made of three fields: `:p` has all the parameters used to start the simulation (including the food web itself), `:t` has a list of all timesteps (including intermediate integration points), and `:B` is a matrix of biomasses for each population (columns) over time (rows). All measures on output described below operate on this object.

The output of simulations can be saved to disc in either the `JSON` (javascript object notation) format, or in the native `jld` format. The `jld` option should be preferred as it preserves the structure of all objects (`JSON` should be used when the results will be analysed outside of `Julia` , for example in `R`). The function to save results is called `BioEnergeticFoodWebs.save` (note that `BioEnergeticFoodWebs.` in front is mandatory, to avoid clashes with other functions called `save` in base `Julia` or other packages).

2.2.7 Measures on output

The `BioEnergeticFoodWebs` package implements a variety of measures that can be applied on the objects returned by simulations. All measures take an optional keyword argument `last` , indicating over how many timesteps before the end of the simulations the results should be averaged.

Total biomass (`total_biomass`) is the sum of the biomasses across all populations. It is measured based on the population biomasses (`population_biomass`).

The number of remaining species (`species_richness`) is measured as the number of species whose biomass is larger than an arbitrary threshold. As `BioEnergeticFoodWebs` uses robust adaptive numerical integrators (such as ODE45 and ODE78), the threshold default value is ϵ, *i.e.* the upper bound of the relative error due to rounding in floating point arithmetic. In short, species are considered extinct when their biomass is smaller than the rounding error. For floating point values encoded over 64 bits (IEEE 754), this is around 10^{-16} (the absolute tolerance of the solver was set to the same value, we kept the default value for the relative tolerance: 0) An additional output related to `species_richness` is `species_persistence` , which is the number of persisting species divided by the starting number of species. A value of `species_persistence` of 1 means that all species persisted. A value of `species_persistence` of 0 indicates that all species went extinct.

Shannon's entropy (`foodweb_diversity`) is used to measure diversity within the food web. This measure is corrected for the total number of populations. This returns values in $]0;1]$, where 1 indicates that all populations have the same biomass. It is measured as

$$H = -\frac{\sum b \times \log(b)}{\log(n)} \,,$$

where n is the number of populations, and b are the relative biomasses ($b_i = B_i / \sum B$).

Finally, we used the negative size-corrected coefficient of variation to assess the temporal stability of biomass stocks across populations (`population_stability`). This function also accepts an additional `threshold` argument, specifying the biomass below which populations are excluded from the analysis. For the same reason as for the `species_richness` threshold, we suggest that this value be set to either the machine's $\epsilon(0.0)$ (*i.e.* the smallest value immediately above 0.0 that the machine can represent), or to 0.0. We found that using either of these values had no qualitative bearing on the results described below. Values close to 0 indicate little variation over time, and increasingly negative values indicate larger fluctuations (relative to the mean standing biomass).

2.3 Implementation and availability

The `BioEnergeticFoodWebs` package is available for the `Julia` programming language, and is continuously tested on the current version of `Julia` , as well as the release immediately before and on the current development version. `Julia` is an ideal platform for this type of model, since it is easy to write, designed for numerical computations, extremely fast, easily parallelized, and has good numerical integration libraries. The package can be installed from the `Julia` REPL using `Pkg.add("BioEnergeticFoodWebs")` . A user manual and function reference are available online at **http://poisotlab.io/BioEnergeticFoodWebs.jl/latest/**, which also gives instructions about installing Julia, the package, and how to get started.

The code is released under the MIT license. This software note describes version `0.2.0` . The source code of the package can be viewed, downloaded, and worked on at **https://github.com/PoisotLab/BioEnergeticFoodWebs.jl**. Potential issues with the code or package can be reported through the *Issues* system. The code is version-controlled, undergoes continuous integration, and has a code coverage of approx. 90% to this date.

2.4 Use cases

All functions in the package have an in-line documentation available at **http://poisotlab.io/BioEnergeticFoodWebs.jl/latest/**, as well as from the `Julia` interface by typing `?` followed by the name of the function. In this section, we will describe three of the aforementioned use cases. The code to execute them is attached as Supp. Mat. to this paper. As all codes in the supplementary material uses `Julia`'s parallel computing abilities, it will differ slightly from the examples given in the paper. For all figures, each point is the average of at least 500 replicates. We conducted the simulations in parallel on 50 Intel Xeon cores at 2.00 Ghz. All random networks were generated using the implementation of the niche model of food webs (Williams & Martinez 2000) provided in `BioEnergeticFoodWebs`.

2.4.1 Effect of carrying capacity on diversity

Starting from networks generated with the niche model with 20 species and connectance of 0.15 ± 0.01, we investigate the effect of increasing the carrying capacity of the resource (on a log scale from 0.1 to 10). We use three values of the α_{ij} parameter, ranging from 0.92 (the interspecific competition is smaller than the intraspecific competition, which should favour coexistence), neutrally stable (intra = interspecific competition = 1), to 1.08 (the intraspecific competition is smaller the interspecific competition, which should favour competitive exclusion).

We run the simulations with the default parameters (given in `?model_parameters`, and in the manual). Each simulation consists of the following code:

```
# We generate a random food web
A = nichemodel(20, 0.15)

# This loop will keep on trying food webs
# until one with a connectance close enough
# to 0.15 is found
while abs(BioEnergeticFoodWebs.connectance(A)-0.15)>0.01
    A = nichemodel(20, 0.15)
end

# Prepare the simulation parameters
for α in linspace(0.92, 1.08, 3)
  for K in logspace(-1, 1, 9)
```

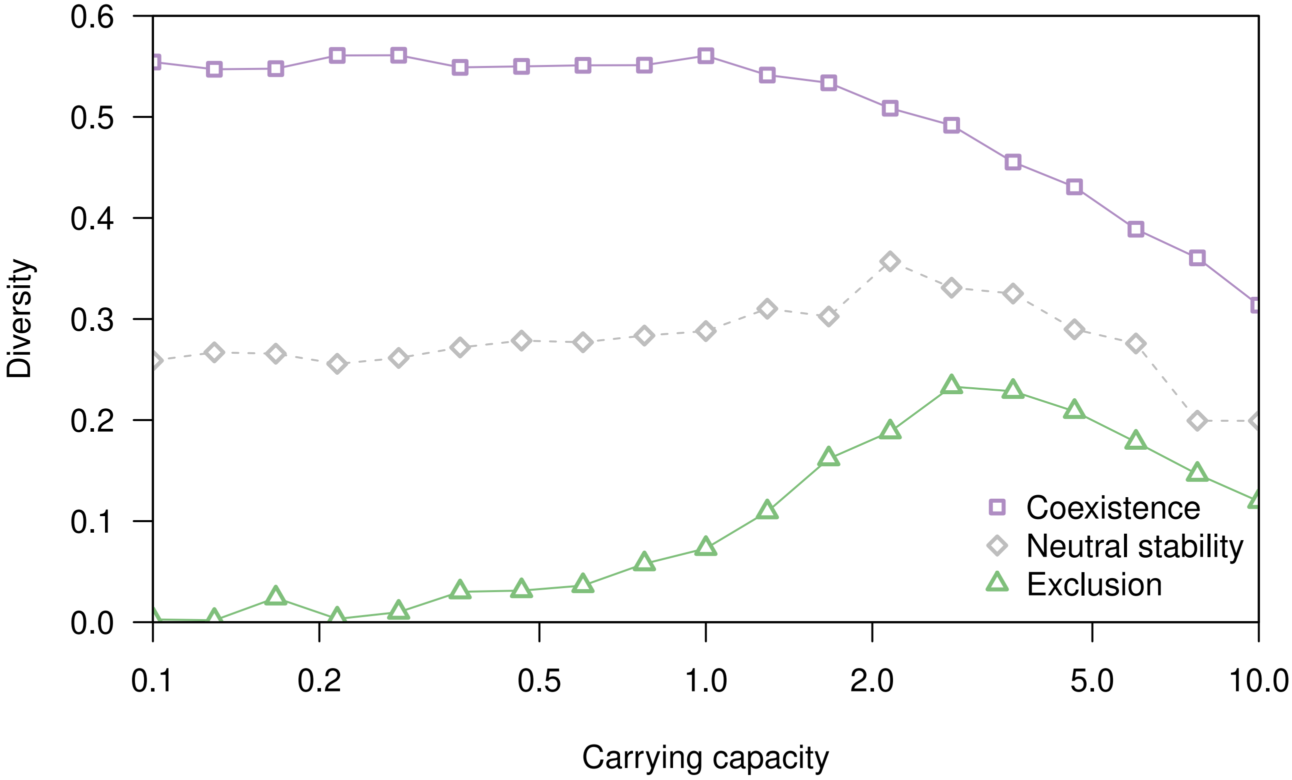

Figure 2.1 Effect of increasing the carrying capacity of the resource for different levels of competition ($\alpha \in [0.9, 1.1]$). For conditions of neutral coexistence or coexistence ($\alpha \leq 1$), diversity is stable until $K \approx 5$. For conditions of competition exclusion ($\alpha > 1$), diversity increases for $K < 5$, and decreases after.

```
    p = model_parameters(A, α = α,
        K=K,
        productivity=:competitive)
    # We start each simulation with
    # random biomasses in ]0;1[
    bm = rand(size(A, 1))
    # And finally, we simulate.
    out = simulate(p, bm, start=0,
          stop=2000, use=:ode45)
    # And measure the output
    diversity = foodweb_diversity(out,
                    last=1000,
                    threshold=eps())
  end
end
```

The results are presented in fig. 2.1.

2.4.2 Effect of consumer-resource body-mass ratio on stability

In fig. 2.2, we illustrate how the effect of body-mass ratio on stabilitydiffers between food webs with invertebrates and ectotherm vertebrate consumers. We measure temporal stability as the negative of the average coefficient of variation over the surviving species:

The body-mass ratio is controlled by the parameter Z (field `Z` in the code), and can be changed in the following way:

```
scaling = logspace(-2, 4, 19) #creates an array with 19 body-mass
   ratio values
# Prepare the simulation parameters
p = model_parameters(A, Z=scaling[i]) #where i is a number from 1 to
    19
```

Which species is an ectotherm vertebrate is controlled by the parameter `vertebrate` of `model_parameters`, which is an array of boolean (true/false) values. In order to have all consumers be ectotherm vertebrates, we use

```
vert = round(Bool,trophic_rank(A).>1.0)
```

so that for each network, we prepare the simulations with

```
# Prepare the simulation parameters
p = model_parameters(A,
      Z=scaling[i],
      vertebrates=vert)
# where i is a number from 1 to 19, as there are
# 19 body-mass ratio values in the scaling array
```

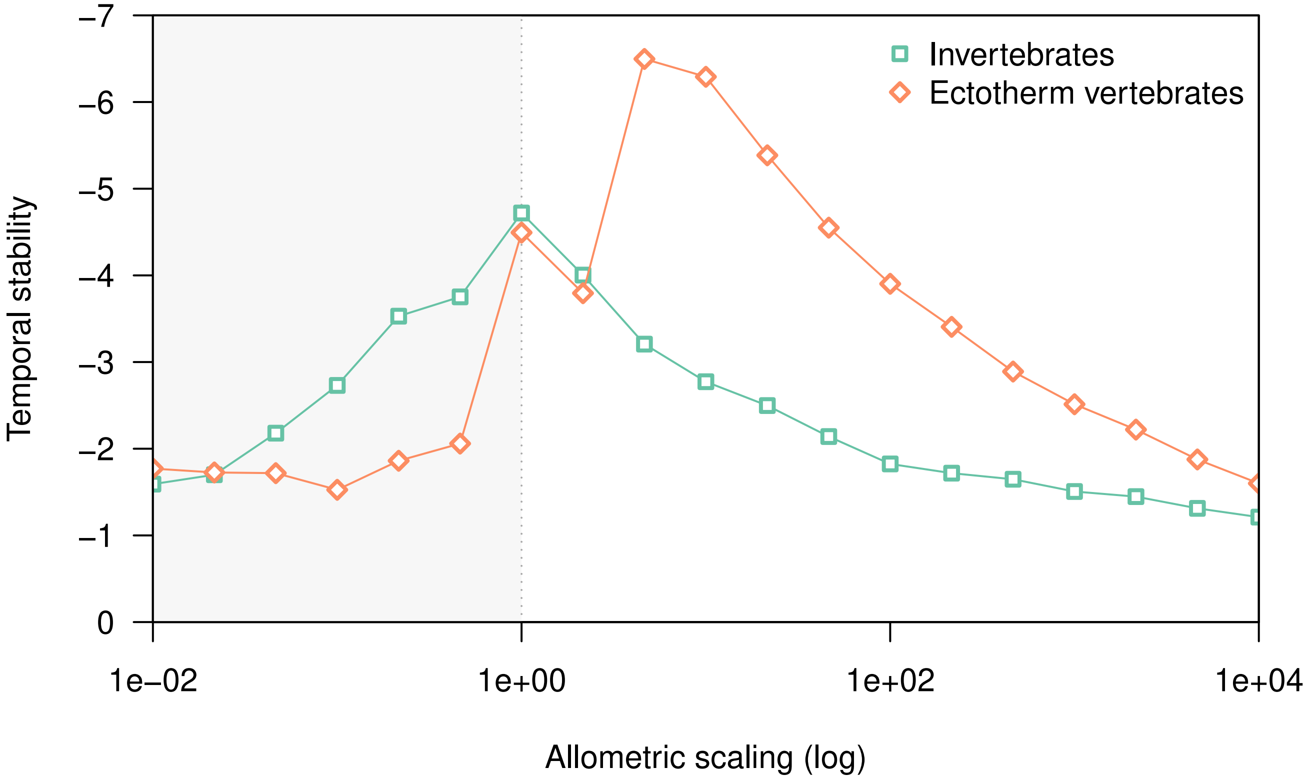

Figure 2.2 The peak of stability, in terms of allometric scaling, differs between vertebrates and invertebrates. Note that the y axis is reversed, since more negative values indicate less variation, and therefore more temporal stability. The shaded area represents negative scaling, *i.e.* predators are smaller than their preys.

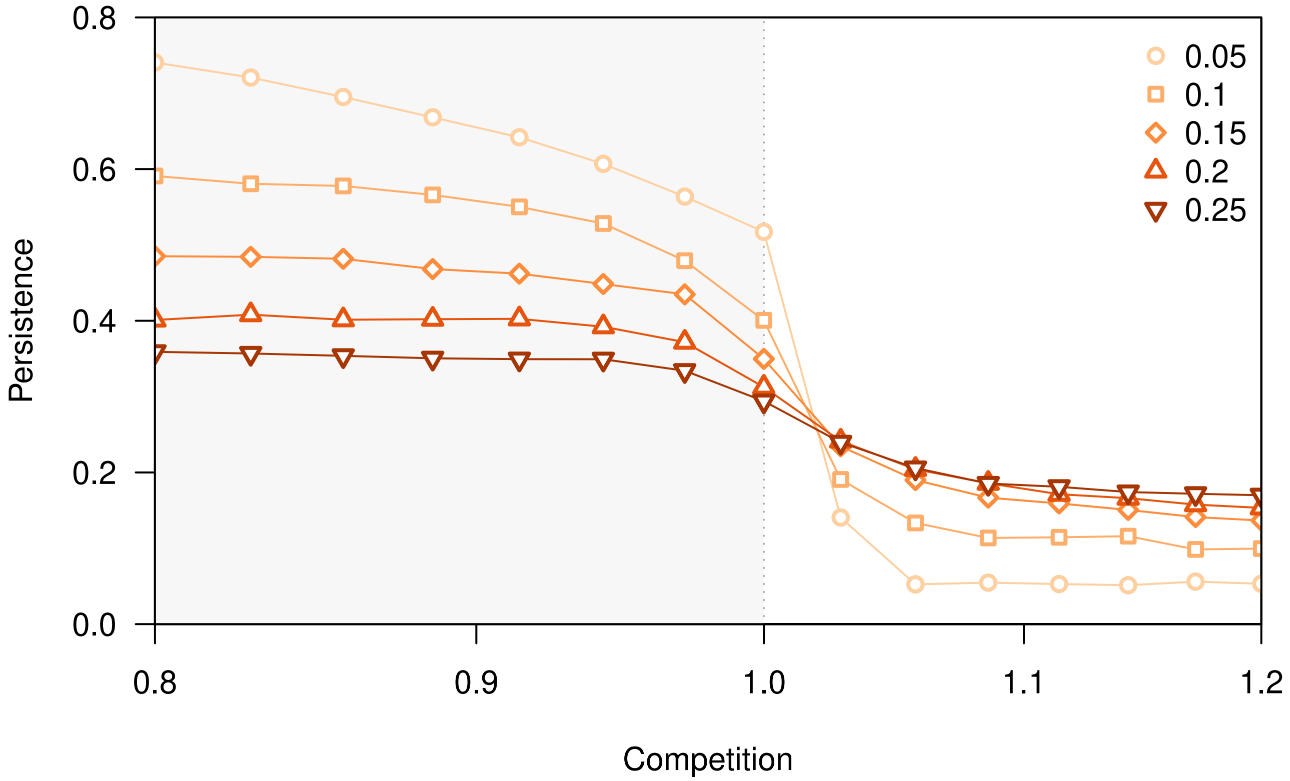

Figure 2.3 Although maximal species persistence is reached for values of interspecific competition lower than unity, the increased trophic control at higher connectances allows coexistence even under stronger competition. The shaded area represents values of α smaller than unity, *i.e.* coexistence is favored.

2.4.3 Effect of connectance on coexistence

We investigate the effect of connectance on species coexistence under different scenarios of interspecific competition rates between producers (fig. 2.3). These simulations therefore measure how the persistence of the entire food web is affected by competition at the most basal trophic level. The persistence is used here as the measure of coexistence.

```
for co in vec([0.05 0.15 0.25])
  # We generate a random food web
  A = nichemodel(20, co)
  while abs(BioEnergeticFoodWebs.connectance(A)-co)>0.01
      A = nichemodel(20, co)
  end
```

```
  # Prepare the simulation parameters
  for α in linspace(0.8, 1.2 , 7)
    p = model_parameters(A, α = α,
    productivity=:competitive)
    bm = rand(size(A, 1))
    # And finally, we simulate.
    out = simulate(p, bm, start=0,
          stop=2000, use=:ode45)
    # And measure the output
    persistence = species_richness(out,
                  last=1000,
                  threshold=eps()) / 20
  end
end
```

Values of α larger than 0 should result in competitive exclusion in the absence of trophic interactions (Williams 2008). Indeed, this is the case when $Co = 0.05$ (only a single consumer remains). Increasing connectance results in more species persisting. Although maximal species persistence is reached for values of interspecific competition lower than unity, the increased trophic control at higher connectances allows coexistence even under stronger competition. The shaded area represents values of α smaller than unity, i.e., coexistence is favoured.

2.5 Conclusion

We have presented `BioEnergeticFoodWebs` , a reference implementation of the bio-energetic model applied to food webs. We provided examples that can serve as templates to perform novel simulation studies or use this model as an effective teaching tool. Because the output can be exported in a language-neutral format (JSON), the results obtained with this model can be analysed in other languages that are currently popular with ecologists, such as `R` , `python` , or `MatLab` . Because we provide a general implementation that covers some of the modifications made to this model over the years, there is a decreased need for individual scientists to start their own implementation, which is both a time consuming and potentially risky endeavour.

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2.6 Supplementary information

2.6.1 List of published papers since 2007 that have used the bio-energetic food-web model.

Reference	Title	Food webs	Model reference	Growth rate function	Functional response	Implementation
Otto et al., 2007	Allometric degree distributions facilitate food-web stability	modules from 5 natural food webs	Yodzis & Ines, 1992	productivity = :species	Type II (:h = 1 and :c = 0)	Not released
Rall et al., 2007	Food-web connectance and predator interference dampen the paradox of enrichment	Cascade model, Niche model and Nested hierarchy model	Yodzis & Ines, 1992	productivity = :species	Type II (:h = 1, :c =0), III (:h = 2, :c = 0) and predator interference, (:h = 1, :c = 1) or gradient (1<:h<2 and 0<:c<4)	Not released
Brose, 2008	Complex food webs prevent competitive exclusion among producer species	Niche model	Yodzis & Ines, 1992	Producer–nutrient model (Brose et al., 2005a,b)	Hill exponent (:h) and predator interference (:c) randomly drawn from truncated normal distributions.	Not released
Williams, 2008	Effects of network and dynamical model structure on species persistence in large model food webs	Cascade model, Niche model Generalized cascade model and random model.	Brose et al. 2006; Williams et al. 2007; Williams and Martinez 2004; Yodzis and Innes 1992	:productivity = :species, :system or :competitive	Type II (:h = 1, :c = 0), Weak type III (:h = 1.2, :c = 0) or Weak predator interference (:h = 1, :c = 0.5)	Not released
Stouffer & Bascompte, 2010	Understanding food-web persistence from local to global scales	Niche model	Yodzis & Ines 1992	productivity = :species	Type II (:h = 1, :c = 0)	Not released
Binzer et al., 2011	The susceptibility of species to extinctions in model communities	Niche model	Yodzis & Ines, 1992	productivity = :system	Hill exponent (:h) and predator interference (:c) randomly drawn from truncated normal distributions.	Not released
Curtsdotter et al., 2011	Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs	Niche model	Brose, 2008; Rall et al., 2008	productivity = :system	Hill exponent (:h) and predator interference (:c) randomly drawn from truncated normal distributions.	Not released
Stouffer & Bascompte, 2011	Compartmentalization increases food-web persistence	Niche model and natural food webs	Yodzis & Ines, 1992	productivity = :species	Type II (:h = 1, :c = 0)	Not released
Kéfi et al., 2016	How Structured Is the Entangled Bank? TheSurprisingly Simple Organization of MultiplexEcological Networks Leads to IncreasedPersistence and Resilience	Natural food web and randomization	Brose, 2008; Yodzis & Ines 1992	productivity = :competitive (see Kéfi et al., 2016 for more details)	Type III (see Kéfi et al., 2016 for more details)	Not released
Iles & Novak, 2016	Complexity Increases Predictability in Allometrically Constrained Food Webs	Niche model	Williams & Martinez, 2004	productivity = :system	Saturating Type III–like functional response :h = 3	Not released
Schneider et al., 2016	Animal diversity and ecosystem functioning in dynamic food webs	Simulated (see Schneider et al., 2016 for more details)	Brose et al., 2008	Producer–nutrient model	Hill exponent (:h) and predator interference (:c) randomly drawn from truncated normal distributions.	Released

Table S2.1 List of published papers since 2007 that have used Yodzis and Ines (1992) mathematical model. The Food Webs column gives the type of data the model was applied to. The growth rate function and functional response columns show how the choice of parameters made in the papers can be reproduced using the BioEnergeticFoodwebs package.

2.6.2 Scripts used to generate the figures in the paper.

Script used to generate fig. 1

```
using DataFrames

# Initialize all cores and set a seed
number_of_cores = 51
while nprocs() < number_of_cores
  addprocs(number_of_cores - nprocs())
end
@everywhere srand(42)

@everywhere using BioEnergeticFoodWebs

@everywhere competition = linspace(0.90, 1.10, 3)
@everywhere k = logspace(-1, 1, 19)

@everywhere replicates = 500
@everywhere conditions = vcat([[[K, com] for com in competition] for
    K in k]...)
@everywhere conditions = vcat([conditions for i in 1:replicates]...)

@everywhere function makesim(k, α)
  # Generate a niche model with 20 species and a connectance of 0.15
    ± 0.01
  A = nichemodel(20, 0.15, tolerance=0.01)
  # Simulate
  p = model_parameters(A, productivity=:competitive, αα=, K=k)
  bm = rand(size(A, 1))
  out = simulate(p, bm, start=0, stop=2000)
  # Get results
  d = foodweb_diversity(out, last=1000)
  s = population_stability(out, last=1000, threshold=eps())
  b = total_biomass(out, last=1000)
  r = species_richness(out, last=1000, threshold=eps()) / 20.0
  # Return20
  return (d, s, b, r)
end

df = DataFrame(
  [Float64, Float64, Float64, Float64, Float64, Float64],
  [:competition, :K, :diversity, :stability, :richness, :biomass],
  length(conditions))

output = pmap((x) -> makesim(x...), conditions)
for k in eachindex(output)
  df[:competition][k] = conditions[k][2]
  df[:K][k] = conditions[k][1]
  df[:diversity][k] = output[k][1]
  df[:stability][k] = output[k][2]
  df[:biomass][k] = output[k][3]
  df[:richness][k] = output[k][4]
end

# Filter results
df = df[!isnan(df[:diversity]),:]
df = df[!isna(df[:diversity]),:]
```

```
df = df[df[:stability] .<= 0.0,:]

writetable("./figures/sm1.dat", df, separator='\t', header=true)
```

Script used to generate fig. 2

```
using DataFrames

# Initialize all cores and set a seed
number_of_cores = 51
while nprocs() < number_of_cores
  addprocs(number_of_cores - nprocs())
end

@everywhere using BioEnergeticFoodWebs

@everywhere Z = logspace(-2, 4, 19)
@everywhere V = vec([true false])

@everywhere replicates = 1000
@everywhere conditions = vcat([[(z, v) for z in Z] for v in V]...)
@everywhere conditions = vcat([conditions for i in 1:replicates]...)

@everywhere function makesim(z, v)
  # Generate a niche model with 20 species and a connectance of 0.15
    ± 0.01
  A = nichemodel(20, 0.15, tolerance=0.01)
  # Simulate
  if v
    #=
    All species with a trophic rank larger than one, i.e., all
   primary producers,
    are vertebrates.
    =#
    vertebrates = trophic_rank(A) .> 1.0
  else
    # If not, all are invertebrates
    vertebrates = falses(size(A, 1))
  end
  p = model_parameters(A, productivity=:system, Z=z, vertebrates=
   round(Bool, vertebrates))
  bm = rand(size(A, 1))
  out = simulate(p, bm, start=0, stop=2000)
  # Get results
  d = foodweb_diversity(out, last=1000)
  s = population_stability(out, last=1000, threshold=-0.01)
  b = total_biomass(out, last=1000)
  r = species_richness(out, last=1000, threshold=eps()) / 20.0
  # Return
  return (d, s, b, r)
end

df = DataFrame(
  [Float64, Bool, Float64, Float64, Float64, Float64],
  [:Z, :vertebrates, :diversity, :stability, :richness, :biomass],
  length(conditions))

output = pmap((x) -> makesim(x...), conditions)
for k in eachindex(output)
```

```
  df[:Z][k] = conditions[k][1]
  df[:vertebrates][k] = conditions[k][2]
  df[:diversity][k] = output[k][1]
  df[:stability][k] = output[k][2]
  df[:biomass][k] = output[k][3]
  df[:richness][k] = output[k][4]
end

# Filter results
df = df[!isnan(df[:diversity]),:]
df = df[!isna(df[:diversity]),:]
df = df[df[:stability] .<= 0.0,:]
#df = df[df[:stability] .>= -5.0,:]

writetable("./figures/sm2.dat", df, separator='\t', header=true)
```

Script used to generate fig. 3

```
using DataFrames

# Initialize all cores and set a seed
number_of_cores = 51
while nprocs() < number_of_cores
  addprocs(number_of_cores - nprocs())
end
@everywhere srand(42)

@everywhere using BioEnergeticFoodWebs

@everywhere competition = linspace(0.8, 1.2, 15)
@everywhere connectance = linspace(0.05, 0.25, 5)

@everywhere replicates = 500
@everywhere conditions = vcat([[[con, com] for com in competition]
   for con in connectance]...)
@everywhere conditions = vcat([conditions for i in 1:replicates]...)

@everywhere function makesim(co, α)
  # Generate a niche model, with relative tolerance
  A = nichemodel(20, co, tolerance=0.01, toltype=:rel)
  # Simulate
  p = model_parameters(A, productivity=:competitive, αα=)
  bm = rand(size(A, 1))
  out = simulate(p, bm, start=0, stop=2000, use=:ode45)
  # Get results
  d = foodweb_diversity(out, last=1000)
  s = population_stability(out, last=1000, threshold=eps())
  b = total_biomass(out, last=1000)
  r = species_persistence(out, last=1000, threshold=eps())
  # Return
  return (d, s, b, r)
end


df = DataFrame(
  [Float64, Float64, Float64, Float64, Float64, Float64],
  [:competition, :connectance, :diversity, :stability, :persistence,
    :biomass],
  length(conditions))
```

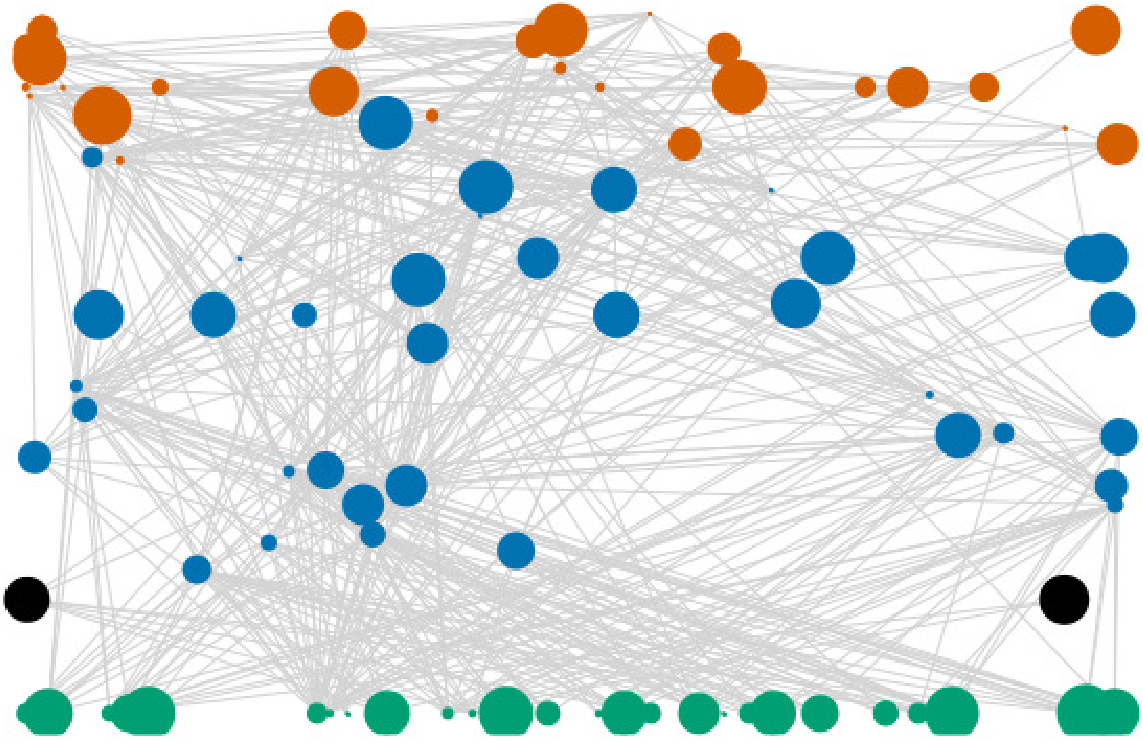
```
output = pmap((x) -> makesim(x...), conditions)
for k in eachindex(output)
  df[:competition][k] = conditions[k][2]
  df[:connectance][k] = conditions[k][1]
  df[:diversity][k] = output[k][1]
  df[:stability][k] = output[k][2]
  df[:biomass][k] = output[k][3]
  df[:persistence][k] = output[k][4]
end

# Filter results
df = df[!isnan(df[:diversity]),:]
df = df[!isna(df[:diversity]),:]
df = df[df[:stability] .<= 0.0,:]

writetable("./figures/sm3.dat", df, separator='\t', header=true)
```

Chapter 3

Analyzing ecological networks of species interactions



Analysing ecological networks of species interactions

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Abstract

Network approaches to ecological questions have been increasingly used, particularly in recent decades. The abstraction of ecological systems – such as communities – through networks of interactions between their components indeed provides a way to summarize this information with single objects. The methodological framework derived from graph theory also provides numerous approaches and measures to analyze these objects and can offer new perspectives on established ecological theories as well as tools to address new challenges. However, prior to using these methods to test ecological hypotheses, it is necessary that we understand, adapt, and use them in ways that both allow us to deliver their full potential and account for their limitations. Here, we attempt to increase the accessibility of network approaches by providing a review of the tools that have been developed so far, with – what we believe to be – their appropriate uses and potential limitations. This is not an exhaustive review of all methods and metrics, but rather, an overview of tools that are robust, informative, and ecologically sound. After providing a brief presentation of species interaction networks and how to build them in order to summarize ecological information of different types, we then classify methods and metrics by the types of ecological questions that they can be used to answer from global to local scales, including methods for hypothesis testing and future perspectives. Specifically, we show how the organization of species interactions in a community yields different network structures (e.g., more or less dense, modular or nested), how different measures can be used to describe and quantify these emerging structures, and how to compare communities based on these differences in structures. Within networks, we illustrate metrics that can be used to describe and compare the functional and dynamic roles of species based on their position in the network and the organization of their interactions as well as associated new methods to test the significance of these results. Lastly, we describe potential fruitful avenues for new methodological developments to address novel ecological questions.

3.1 Introduction

Al-Jahiz was perhaps the first scientist to provide, as early as in the eighth century, a description of a food chain (Egerton 2002). About a thousand years later, Camerano (1880) introduced the idea that the diversity of animal forms, and therefore biological diversity itself, can only be explained when framed in the context of interrelationships among species. Seminal work by Patten (1978) and Ulanowicz (1980) suggested that the structure of networks can approximate information on theoretical constraints on community assembly, and helped generate interest in the application of network science to ecology. "Network-thinking" now permeates studies in ecology and evolution (Proulx et al. 2005), and is one of the fastest growing ecological disciplines (Borrett et al. 2014), accounting for 5% of all published papers in 2012. Network-based approaches are gaining momentum as one of the most helpful tools for the analysis of community structure (Poisot et al. 2016b), because they offer the opportunity to investigate, within a common formal mathematical framework, questions ranging from the species level to the community level (Poisot et al. 2016b). Applying network approaches to a variety of ecological systems, for example hosts and parasites (Poulin 2010), or bacteria and phage (Weitz et al. 2013), yields new methodological and biological insights, such as the observation that networks tend to be locally nested but regionally modular (Flores et al. 2013), which suggests that different ecological and evolutionary regimes are involved at different scales. Despite this long-standing interest, the application of measures grounded in network science is still a relatively young field (in part because the computational power to perform some of these analyses was largely unavailable in the early days of the field). This comes with challenges to tackle. First, there is a pressing need for additional methodological developments, both to ensure that our quantitative analysis of networks is correct, and that it adequately captures the ecological realities that are, ultimately, of interest. Second, we need to understand better the limitations and domain of application of current methods. Yet, there is a lack of a consensus on what constitutes a "gold standard" for the representation, analysis, and interpretation of network data on ecological interactions within the framing of specific ecological questions; *i.e.* which of the many available measures actually hold ecological meaning. All things considered, the analysis of ecological networks can be confusing to newcomers as well as researchers who are more well versed in existing methods.

Most notions in community ecology, including the definition of a community (Vellend 2010; Morin 2011), and several definitions of a niche (Holt 2009; Devictor et al. 2010), emphasize the need to study the identity of species and their interactions simultaneously (although ecological network analysis can be critiqued for ignoring species identity in many instances). Studies of ecological communities can therefore not discard or disregard interactions (McCann 2007a), and using network theory allows researchers to achieve this goal. With the existence of methods that can analyze (large) collections of interactions, this approach is methodologically tractable. Graph theory provides a robust and well formalized framework to handle and interpret interactions between arbitrarily large (or small) numbers of species. Theoretical analyses of small assemblages of interacting species (e.g., "community modules", Holt 1997a) have generated key insights into the dynamics of properties of ecological communities. We expect there is even more to gain by using graph theory to account for structure at increasingly high orders of organization (e.g., more species, larger spatial or temporal scales), because there is virtually no upper bound on the number of nodes (species) or edges (interactions) it can be applied to, and theory on large graphs can help predict the asymptotic behaviour of ecological systems. In short, although graph theory may appear as overwhelmingly complicated and unnecessarily mathematical, it allows us to express a variety of measures of the structure of networks that can be mapped onto ecologically relevant questions.

Applying measures from network science to ecological communities can open three perspectives (Poisot et al. 2016b). First, the multiplicity of measures confers additional tools to describe ecological communities. This can reveal, for example, unanticipated ways in which communities differ. Second, these measures can provide new explanatory variables to explain how ecological communities function. The question of stability, for example, has been approached through the analysis of empirical food webs to question long-standing theoretical results (Jacquet et al. 2013). Finally, and this is a new frontier in network studies, they open the ability to predict the structure of ecological communities, through the prediction of interactions (Desjardins-Proulx et al. 2017; Stock et al. 2017). The domain of application of ecological networks is as vast as the domain of application of community ecology; but ensuring that network measures deliver their full potential of advancing our understanding of ecological systems requires that they are well understood, and well used. Because of advances in graph theory, and the availability of more efficient computational methods, the exploration of large networks is now feasible. While this may not be immediately useful to macrobe-based research, microbial ecology, through sequencing, is able to generate data sets of immense size that can be analysed with the tools we present here (Faust & Skvoretz 2002).

This review provides an assessment of the state of methodological development of network science applied to ecological communities. Taking stock of the tools available, their strengths and limitation, is a necessary first step to determine how we can best analyse data from ecological networks and improve in the future our analyses of their consequences on dynamic ecological processes (see Jordano & Bascompte 2013 for mutualistic systems; Poulin 2010 for parasites; McCann 2012 for food webs; or Dormann et al. 2017 for a recent overview). In this review, we highlight areas in which future research is needed, so as to eventually establish a comprehensive framework for how ecological networks can be analysed. The measures presented herein do not represent all the measures that are available for ecological networks; instead, they represent a core set of measures that are robust, informative, and can be reasoned upon ecologically. While this review does not present the entire framework for ecological network analysis, we are confident that it provides a solid foundation for its future development, and that the recommendations we lay out should be used by future studies. We have organized the measures by broad families of ecological questions. What is the overall structure of ecological networks? How can we compare them? What are the roles of species within networks? How similar are species on the basis of their interactions? How can we assess the significance of measured values? What are emerging questions for which we lack a robust methodology? This order mimics the way networks are usually analysed, starting from community-level structure, and going into the species-level details.

3.2 What are species interaction networks?

Identifying interactions across ecological entities can be done in a variety of ways, ranging from literature survey and expert knowledge, direct or indirect observation in the field using gut content (Carscallen et al. 2012), stable isotopes, molecular techniques such as meta-barcoding and environmental DNA (Evans et al. 2016; O'Donnell et al. 2017), to modelling based on partial data or mechanistic models. Depending on how they were assembled, species interaction networks can represent a multitude of ecological realities. When based on field collection (Morand et al. 2002; Bartomeus 2013; Carstensen et al. 2014), they represent realized interactions, known to have happened (unreported interactions can be true or false absences, depending on sampling effort among other things). Another common method is to 'mine' the literature (e.g., Havens 1992; Strong & Leroux 2014) or databases (Poisot et al. 2015b), to replace or supplement field observations. In this situation, species interaction networks describe potential interactions: knowing that two species have been observed to interact once, there is a chance that they interact when they co-occur. Another more abstract situation is when interactions are inferred from a mixture of data and models, based on combinations of abundances (Canard et al. 2014), body size (Gravel et al. 2013; Pires et al. 2015), or other traits (Crea et al. 2015; Bartomeus et al. 2016). In this situation, species interaction networks are a prediction of what they could be. In keeping with the idea of 'networks as predictions', a new analytical framework (Poisot et al. 2016a) allows working directly on probabilistic species interaction networks to apply the family of measures presented hereafter.

Interactions are compiled and resolved (and subsequently assembled in networks) for a multitude of taxonomic and organisational levels (Thompson & Townsend 2000): individuals (Araújo et al. 2008; Dupont et al. 2009, 2014; Melián et al. 2014); species (Morand et al. 2002; Krasnov et al. 2004); at heterogeneous taxonomic resolutions, including species, genera, and more diffusely defined 'functional' or 'trophic' species (Martinez et al. 1999; Baiser et al. 2012); groups of species on the basis of their spatial distribution (Baskerville et al. 2011). This is because species interaction networks are amenable to the study of all types of ecological interactions, regardless of the resolution of underlying data: mutualistic, antagonistic, competitive, and so on. Recent developments made it possible to include more than one type of interaction within a single network (Fontaine et al. 2011a; Kéfi et al. 2012), allowing greater ecological realism in representing communities, which encompass several types of interactions (e.g., plants are consumed by herbivores, but also pollinated by insects). Such networks are instances of multigraphs (in which different types of interactions coexist). Another development accounts for the fact that ecological interactions may have effects on one another, as proposed by e.g., Golubski & Abrams (2011); these are hypergraphs. Hypergraphs are useful when interactions rely, not only on species, but also on other species interactions: for example, an opportunistic pathogen may not be able to infect a healthy host, but may do so if the host's immune system is already being compromised by another infection. Hence it is not only species, but also their interactions, which interact. Such higher-order interactions can be detected through comparing observed species density or performance to that obtained under a dynamic model without higher-order interactions (Billick & Case 1994; Mayfield & Stouffer 2017). As using these concepts in ecological research represents a recent development, there is little methodology to describe systems represented as multigraphs or hypergraphs, and we will only mention them briefly here. In a way, methodological developments on these points are limited by the lack of data to explore their potential. As the interest among network ecologists will increase for systems in which the current paradigm of species–species interactions falls short, we expect that the inflow of data will stimulate the emergence of novel methods.

Formally, all of these structures can be represented with the formalism of graph theory. A graph G is defined as an ordered pair (V, E), where every element of E (the edges) is a two-element subset of V (the nodes). From this simple structure, we can measure a large number of properties (see e.g., Newman 2010 for an introduction). A simple graph contains neither self-edges (a node is linked to itself) or multiedges (the same two nodes are linked by more than one type of edge), whereas a multigraph contains at least one multiedge. As we illustrate in fig. 3.1, edges can be directed (e.g., A eats B), or undirected (e.g., A and B compete); unweighted (e.g., A pollinates B) or weighted (e.g., A contributes to 10% of B's pollination). In the context of studying ecological interactions, V is a set of ecological objects (taxonomic entities, or other relevant components of the environment), and E are the pairwise relationships between these objects. As both the strengths of interactions and their direction are highly relevant to ecological investigations, data on species interactions are most often represented as networks: directed and weighted graphs. We use network as a synonym for "graph" throughout. Species interaction networks can, finally, be represented as unipartite or bipartite networks. Unipartite networks are the more general case, in which any two nodes can be connected; for example, food webs or social networks are unipartite (Post 2002; Dunne 2006). Unipartite networks can represent interactions between multiple groups; for example, food webs can be decomposed into trophic levels, or trophic guilds. Bipartite networks, on the other hand, have nodes that can be divided in disjointed sets T (top) and B (bottom), such that every edge goes from a vertex from T, to a vertex from B; any ecological community with two discrete groups of organisms can be represented as a bipartite network (e.g. plant and mutualists, Jordano & Bascompte 2013; parasites and hosts, Poulin 2010; phage and bacteria, Weitz et al. 2013). It is possible to represent k-partite networks, i.e. networks with k discrete "levels". This formalism has been used for resources/consumers/predators (Chesson & Kuang 2008), and other plant-based communities (Fontaine et al. 2011b). Tripartite networks

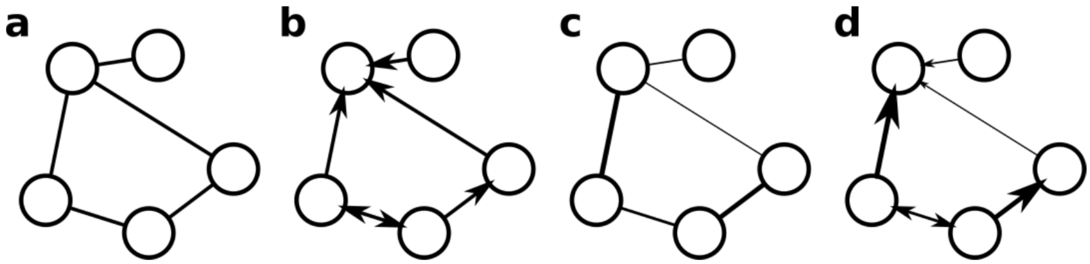


Figure 3.1 Differences between (un)weighted and (un)directed graphs. Graphs (A) and (C) are undirected, and graphs (A) and (B) are unweighted. Arrows thickness in graphs (C) and (D) represents the strength of the link.

are usually analyzed as collections of bipartite networks, or as unipartite networks. There still exists few data on ecological k-partite networks, and it is therefore difficult to establish solid recommendations about how they can be analyzed; this is a part of the field in which methodological developments are still needed and ongoing.

Networks can be represented using their adjacency matrix ($\mathbf{A}$). For a unipartite network containing S species, $\mathbf{A}$ is a square matrix of dimensions (S, S). For a bipartite network containing $T + B$ species, the dimensions are (T, B), and the $\mathbf{A}$ matrix is usually referred to as the incidence matrix. In both cases, the elements a_{ij} of the matrix indicate whether species i interact with species j. In unweighted networks, $a_{ij} = 1$ when i and j interact and 0 otherwise. In weighted networks the strength of the interaction is given, instead of being set to unity. Note that in weighted networks, the strength of the interaction is not necessarily between 0 and 1; if the strength of interactions depicts the raw effect of one population on another, then it can take on both negative and positive values. The adjacency matrix is symmetrical for undirected networks, because $a_{ij} = a_{ji}$. In simple networks, the matrix diagonal is empty as there are no self-edges (which, ecologically, could represent autophagy, breastfeeding in mammals or cannibalism). We would like to note that $\mathbf{A}$ is not the de facto community matrix: in some situations, it can be more profitable to describe the community using its Jacobian matrix, i.e., one in which a_{ij} represents the net effect of species i on species j (May 1972, 1974b; Gravel et al. 2016b; Monteiro & Faria 2016; Novak et al. 2016).

3.3 What can we learn with ecological networks?

Here, unless otherwise stated, we will focus on describing measures of the structure of unweighted, directed networks (i.e., either the interaction exists, or it does not; and we know in which direction it points), to the exclusion of quantitative measures that account for the strength of these interactions. In most cases, quantitative variations of the measures we present do exist (see e.g., Bersier et al. 2002), and share a similar mathematical expression. We think that focusing on the simplifying (yet frequently used) unweighted versions allows one to develop a better understanding, or a better intuition, of what the measure can reveal. There is a long-standing dispute (Post 2002) among ecologists as to whether "arrows" in networks should represent biomass flow (e.g., from the prey to the predator) or interaction (e.g., from the predator to the prey). Because not all interactions involve biomass transfer, and because networks may be used to elucidate the nature of interactions, we will side with the latter convention. In general, we will assume that the interaction goes from the organism establishing it to the one receiving it (e.g., from the pollinator to the plant, from the parasite to the host, etc.).

3.3.1 What do communities look like?

Order, size and density During the last decades, various network measures have been developed to characterize the general structure of interacting communities, capturing both species identity and their interactions (Dunne et al. 2002b; Montoya et al. 2006; Allesina & Pascual 2007; Thompson et al. 2012). Most of these measures encompass and supplement usual measurements in community ecology. In addition to how many species there are, and which species are in local area, knowledge of their interactions is an additional layer of information that network measures exploit to quantify biodiversity.

A first descriptor of a network is its order (S), i.e., the total number of nodes. If nodes are species, order measures the species richness of the community described by the network G. The total number of interactions (L) is the size of the network. From these two measures is computed the linkage density $\frac{L}{S}$ (e.g., Bartomeus 2013), which is the mean number of interactions per node – or simply, if a random species is selected, how many interactions it would be expected to have. Linkage density should be considered with caution as it can be misleading: the distribution of interactions among nodes in species interaction networks is rarely uniform or normal (Williams 2011), and a minority of species are known to establish a majority of interactions (Dunne et al. 2002a). Moreover L is known to scale with S^2 (Cohen & Briand 1984; Martinez 1992), at least in trophic interaction networks.

This observation that L scales with S^2 has cemented the use of an analog to linkage density, the connectance (Co), as a key descriptor of network structure (Martinez 1992). Connectance is defined as $\frac{L}{m}$, i.e., the proportion of established interactions (L), relative to the possible number of interactions m. The value of m depends of the type of network considered. In a unipartite directed network, m is S^2. In a directed network in which species cannot interact with themselves, m is $S(S-1)$. In an undirected network, m is $S\frac{S-1}{2}$ if the species cannot interact with themselves, and $S\frac{S+1}{2}$ if they can. In a bipartite network, m is $T \times B$, the product of the number of species at each level. The connectance varies between 0 if the adjacency matrix is empty to 1 if its entirely filled. It is also a good estimate of a community sensitivity to perturbation (Dunne et al. 2002a; Montoya et al. 2006) as well as being broadly related to many aspects of community dynamics (Vieira & Almeida-Neto 2015). Although simple, connectance contains important information regarding how links within a network are distributed, in that many network properties are known to covary strongly with connectance (Poisot & Gravel 2014; Chagnon 2015), and the fact that most ecological networks "look the same" may be explained by the fact that they tend to exhibit similar connectances (fig. 3.2). Poisot & Gravel (2014) derived the minimum number of interactions that a network can have in order for all

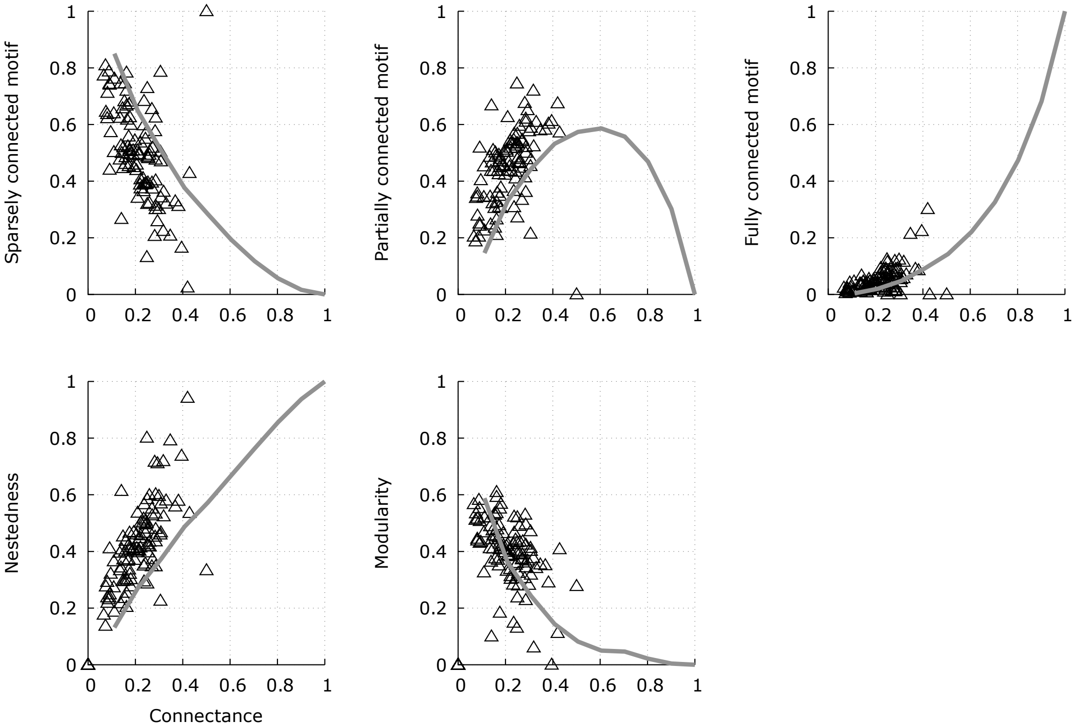


Figure 3.2 To illustrate the strong relationship betweeen connectance and other network measures, we measured the nestedness using η, modularity (best partition out of 100 runs), and the relative frequencies of three bipartite motifs (white, sparsely connected; grey, partially connected; black, fully connected) in 102 pollination networks. The sparsely connected motif represents two independent interactions. The partially connected motif represents the addition of one interaction to the sparsely connected one, and the fully connected motif includes the addition of another interaction. All of these measures have a strong covariance with connectance, and for this reason, the comparison of networks with different connectances must rely on randomizations. For data, methods, and code see **https://osf.io/82ypq/**.

species to have at least one interaction. This allows us to express connectance in the [0; 1] interval, where 0 indicates that the network has the least possible number of interactions.

Interactions repartition within the networks The majority of real-world species interaction networks are highly heterogeneous with regard to interactions distribution among nodes. It is possible to study the degree distribution of the network (the distribution of the number of interactions per node, see paragraph below). The way interactions are organized (distributed) among the nodes reflects ecological constraints and can be studied using various methods.Quantitative measures of different structures have been developed from graph theory and have played a growing role in understanding the evolution and functioning of ecological communities – in particular, because these measures add a small amount of information (comparatively to measures presented later below), they are a natural first step in moving away from a species-centric view of community into the arguably more realistic species-and-interactions view that networks capture well.

If the degree of a node is its number of interactions, then the degree distribution $P(k)$ measures the probability that a species has k interactions within the network. The degree distribution can be calculated as $P(k) = N(k)/S$ where $N(k)$ is the number of nodes with k interactions, and S is the total number of species in the network. The degree distribution allows identification of important nodes, such as potential keystone species (Sole & Montoya 2001 ; Dunne et al. 2002b), generalists, and specialist species (Memmott et al. 2004). In directed networks, the degree distribution can be divided into in-degree and out-degree. These respectively correspond to species vulnerability (e.g., number of predators in food webs) and generality (e.g., number of resources in food webs). It is often assumed that the distribution of degree in networks should resemble a power law (Strogatz 2001; Caldarelli 2007). In other words, the proportion $\mathrm{P}(k)$ of nodes with degree k should be proportional to $k^{-\gamma}$ (but see see Jordano et al. 2003 – a truncated power law may be a more accurate description). Assuming that power laws are an appropriate benchmark is equivalent to assuming that ecological networks are structured first and foremost by preferential attachment, and that deviation from power-law predictions suggests the action of other factors. Dunne et al. (2002a) found that, at least in food webs, ecological networks tend not to be small-world or scale-free (i.e., having a specific degree distribution; Caldarelli 2007), but deviate from these rules in small yet informative ways (specifically, about prey selection or predator avoidance). Opportunistic attachment and topological plasticity have been suggested as mechanisms that can move the system away from predictions based on power laws (Ramos-Jiliberto et al. 2012; Ponisio et al. 2017). We suggest that deviations from the power law be analysed as having intrinsic ecological meaning: why there are more, or fewer, species with a given frequency of interactions may reveal reasons for and/or constraints on particular species interactions.

The network diameter gives an idea of how quickly perturbations may spread by providing a measure of how dense the network is. Diameter is measured as the longest of all the shortest distances (d_{ij}) between every pair of nodes in the graph (Albert & Barabási 2002), where d_{ij} is the length of the shortest path (sequence of interactions) existing between the nodes i and j. A small diameter indicates the presence of a densely connected nodes, or hubs, hence fast propagation between nodes which may make the network more sensitive to perturbation (e.g. rapid spread of a disease; Minor et al. 2008). The diameter is relative to the number of nodes in the network, since it relies on counting the number of edges in a path, which may become larger as the network order increases. To overcome this issue, the diameter can also be measured as average of the distances between each pair of nodes in the network.

Aggregation of nodes based on their edges From the heterogeneous repartition of interactions between nodes in species interaction networks, certain structures and groupings of interactions around nodes emerge. While the degree distribution hints at how edges are organized around single nodes, one can frame this question at the scale of the entire network. It is likely that other structures will appear when multiple nodes are considered at once. This can be done by analyzing what types of relationships the nodes (representing species, etc.) are typically embedded in (e.g., competition, intraguild predation), through the analysis of motifs distribution, or by determining if there are nodes found in dense clusters or non-overlapping compartments, forming modular communities.

Species interaction networks can be decomposed into smaller subgraphs of n species, called motifs (Milo 2002). The smallest modules to which they can be decomposed are three-species motifs (Holt 1997a). The relative frequencies of each of these motifs holds information about network structure. There are 13 possible three-nodes motifs in directed networks, each representing a different relationship between three nodes, such as competition between A and B for a shared resource C ($A \rightarrow C \leftarrow B$), or a linear chain between A, B and C ($A \rightarrow B \rightarrow C$). Among these 13 motifs, some are present in species interaction networks with a lower or higher frequency that what is expected in random networks. Motif distributions are characteristic of network type (neuronal, electrical, social, ecological, and so on). In food webs for example, motifs under- and over-representation has been found to be consistent across different habitats (Camacho et al. 2007; Stouffer et al. 2007; Borrelli 2015). In ecological networks, motifs have been referred to as the basic building blocks of communities, as they represent typical relationships between species. Studying their distribution (i.e., how many of each type of motif there is this network) offers an opportunity to bridge the gap between two traditional approaches (Bascompte & Melián 2005), namely the study of the dynamics of simple modules such as omnivory or linear food chain (Pimm & Lawton 1978; Holt 1996; McCann et al. 1998), and the analysis of aggregated metrics describing the community as a whole. Motif distributions have been used to study the processes underlying the assembly and disassembly of ecological communities (Bastolla et al. 2009), as well as of the link between community's structure and dynamics (Stouffer & Bascompte 2011). More recently, motifs have also been used to define species' trophic roles in the context of their community (Baker et al. 2014) and to link this role to the network's stability (Borrelli 2015).

The clustering coefficient is useful to estimate the "cliquishness" of nodes in a graph (Watts & Strogatz 1998) – that is their grouping in closely connected subsets. It measures the degree to which the neighbours of a node are connected (the neighbourhood of a node i is composed of all of the nodes that are directly connected to i). In other words, it gives an idea of how likely it is that two connected nodes are part of a larger highly connected group or "clique". Two different versions of the clustering coefficient (CC) exist. First, it can be defined locally, for each node i (Watts & Strogatz 1998). In this case $cc_i = \frac{2N_i}{k_i(k_i-1)}$ where k_i is i's degree (its number of neighbours) and N_i is the total number of interactions between i's neighbours. It describes the fraction of realized edges between i's neighbours and thus varies between 0

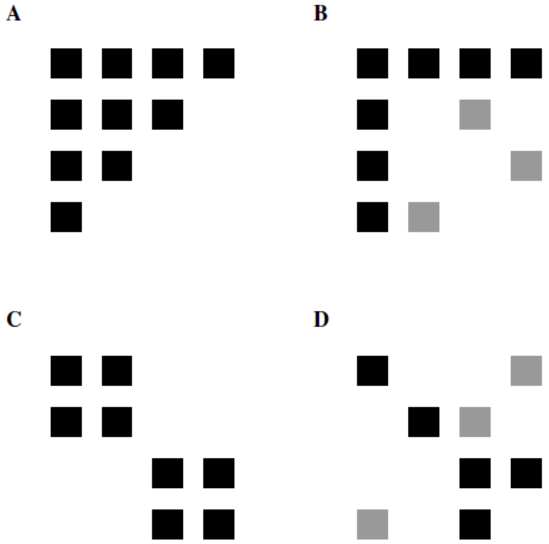


Figure 3.3 Illustration of the nested and modular structure of networks, represented as matrices. A is a perfectly nested matrix; in B, three interactions (in grey) have been displaced to lose the perfectly nested structure. C is a perfectly modular network; in D, three interactions have been displaced to lose the modular structure.

(none of i's neighbours are connected) and 1 (all of them are connected, forming a "clique"). From this measure, we can calculate the average local clustering coefficient: $CC_1 = \frac{\sum_i c_i}{S}$ where S is the total number of nodes. This first version describes the "cliquishness" of a typical neighbourhood, but has the drawback of giving more influence to nodes with a small degree. Nevertheless, the clustering coefficient provides a way of characterising the structure of the graph through the analysis of CC_k, which is the average of the cc_i of all nodes of degree k, and specifically of the distribution of CC_k across multiple values of k. The clustering coefficient can also be defined globally, for the entire graph (Soffer & Vazquez 2005; Saramäki et al. 2007) and is calculated as follows $CC_2 = \frac{3N_t}{N_c}$, where N_t is the number of triangles in graph G (a is connected to b and c, b to a and c and c to a and b) and N_c is the number of three-node subgraphs (e.g., a is connected to b and c, b and c are connected to a but not to each other). Kim (1993) suggested that this property of a network can be used to infer competition, but this has to our knowledge received little attention in ecology.

Whereas clustering analysis gives information about the grouping of nodes within their immediate neighbourhood (but no information about the identity of nodes in this neighbourhood), a measure of modularity gives a similar information at a larger scale (Gauzens et al. 2015). Network modularity measures how closely connected nodes are divided in modules, also called compartments (Olesen et al. 2007). A module is defined as a subsystem of non-overlapping and strongly interacting species (see fig. 3.3, matrices C and D for a comparison of the structures of modular and non-modular matrices). The modular structure of graphs has been studied because of its dynamical implications, in that modularity promotes stability by containing perturbations within a module, thereby constraining their spreading to the rest of the community (Stouffer & Bascompte 2010, 2011). This has been a key argument in the diversity-stability debate (Krause et al. 2003). A major challenge when studying the modularity of species interaction networks is to find the best subdivision of the network. Several methods have been developed for this purpose, which can be classified into three categories: i) classical optimization of a modularity function that maximizes link density within modules (Guimerà et al. 2004; Newman 2004; Newman & Girvan 2004; Guimerà & Amaral 2005a, 2005b), ii) probability mixture strategies (stochastic blockmodels, usually referred to as group model in ecology; Holland et al. 1983; Allesina & Pascual 2009a) and iii) modular flow analysis based on maps of random walk (Rosvall & Bergstrom 2008; Rosvall et al. 2009; Farage et al. 2020). These usually resulting in different groupings, reflecting the fact that there is not one true grouping of nodes in ecological networks. The method must thus be chosen carefully to fit the type of information one wants to reveal.

The optimization of a modularity function is by far the most popular in ecology The principle underlying this function is to find the optimal subdivision that maximizes the number of interactions within modules while minimizing the number of interactions between modules. The calculated modularity is then compared with a null model that has the same number of links and nodes, with the links connected to each other randomly. Modularity optimization has a resolution limit (in that its performance decreases with the size of the network) making it less reliable for large species interaction networks (Fortunato & Barthélemy 2007); there are methods designed specifically to work on thousands of nodes and more (see e.g. Liu & Murata 2009). To compare outcomes of different modularity measurements, it is possible to use an a posteriori method. In a network where modules are already found, the realized modularity (Q'_R) measures the proportion of interactions connecting nodes within modules (Poisot 2013). This is expressed as

$$Q'_R = 2 \times \frac{W}{L} - 1 \,, \tag{3.1}$$

where W is the number of interactions within modules, and L is the total number of interactions. This takes on a value of 1 when modules are disconnected from one another (which is not true of other modularity functions that account for the probability of establishing an edge). This measure can take on negative values if there are more interactions between modules than within them, which can be viewed as a non-relevant partitioning of the community.

Nestedness Species interaction networks can also present a nested structure (see fig. 3.3, matrices A and B for a comparison of the structures of nested versus non-nested matrices), where the species composition of small assemblages are subsets of larger assemblages. In food webs, a nested structure occurs when the diet of the specialist species is a subset of the diet of the more generalist species – and where the predators of species are nested as well. The analysis of nestedness has revealed ecological and evolutionary constraints on communities. For example, it has been hypothesized that a nested structure promotes greater diversity by minimizing competition among species in a community (Bastolla et al. 2009). Various metrics have been developed to quantify nestedness (Ulrich 2009; Ulrich et al. 2009). Most are based on the principle that when a matrix is ordered by rows and columns (that is descending in rank from above and from the left) a nested network will present a concentration of presence data in the top-left corner of the matrix, and a concentration of absence data in the opposite corner [see

Staniczenko et al. (2013) for an exception; see fig 3.3C]. Numerous studies (Rodriguez-Girones & Santamaria 2006; Fortuna et al. 2010; Flores et al. 2011) use the proportion of unexpected presence or absence in the matrix to quantify nestedness. Seemingly the most widely used measure of nestedness is based on overlap and decreasing fills (NODF), as suggested by Almeida-Neto et al. (2007); Bastolla et al. (2009) suggested that η can complement NODF, in that η does not require a re-ordering of the nodes (i.e., there is no need to put the most densely connected nodes first, and the least densely connected nodes last). As per Bastolla et al. (2009), η is defined as:

$$\eta(\mathbf{A}) = \frac{\sum_{i<j} n_{ij}}{\sum_{i<j} \mathrm{minimum}(n_i, n_j)} \tag{3.2}$$

where n_{ij} is the number of common interactions between species i and j, and n_i is the number of interactions of species i. Note that this formula gives the nestedness of rows with regard to the columns, though one can also measure the nestedness of columns with regard to rows as $\eta(\mathbf{A}')$, and calculate the nestedness of the whole system as the average of these two values. We suggest that, since it does not rely on species re-ordering, η can be used over NODF or other nestedness measures. There are some caveats to this argument, however. First, the number of permutations for NODF is known, and for species-poor networks, they can be computed in a reasonable time. Second, NODF can help understanding how different orderings of the matrix (e.g., informed by species traits such as interaction strength or forbidden links)contributes to nestedness – if this is the question of interest, then NODF is the logical choice (Krishna et al. 2008). Once ordered by degree, NODF and η are identical (with the exception that NODF accounts for decreasing fill, whereas η does not). Finally, η has the undesirable property of always giving the same value depending only on the degree distribution. Therefore, any permutation of a network that maintains the degree distribution will give the same value of η, which greatly impedes hypothesis testing.

Intervality A last measure of the structure of species interaction networks is their intervality. A network is "interval" when it can be fully explained by one dimension (trait). An interval food web with species ordered by their body mass, as an example, has predator eating a consecutive range of prey, that all fall into a range of body masses (Eklöf & Stouffer 2015), or are closely related from a phylogenetic standpoint (Eklöf & Stouffer 2015). The first step in calculating intervality is to identify a common trait along which nodes can be ordered. This can be body mass in the case of food webs, but can also be a property derived from their position in the network, such as their degree; indeed, a nested bipartite network is interval when species are organized by decreasing degree. Intervality then measures how well interactions of all species can be described by this trait. Most unipartite ecological networks are close to being interval with one or several dimensions, such as defined by body size (Zook et al. 2011) or arbitrary traits derived from the interactions themselves (Eklöf et al. 2013). There are several methods to quantify a network's intervality. Cattin et al. (2004) quantified the "level of diet discontinuity" using two measures: (i) the proportion of triplets (three species matrix) with a discontinuous diet (i.e., at least one species gap), in the whole food web (D_{diet}), and (ii) the number of chordless cycles (C_{y_4}). A cycle of four species (a graph cycle is a subset of species, here 4, that are connected by a continuous path of interactions such that the first species is also the last)is considered as chordless if at least two species out of the four are not sharing prey, so the diets cannot be totally interval. Nevertheless, these two measures only give a local estimation of intervality. Stouffer et al. (2006) proposed to measure the intervality of the entire network by re-organizing the interaction matrix to find the best arrangement with the fewest gaps in the network. This is a stochastic approach that by definition does not guarantee finding the global optimum, but has the benefit of working at the network scale rather than at the scale of triplets of species.

3.3.2 How are communities different?

Detecting spatial and temporal variation in ecological networks, and associating these variations with environmental factors, may yield insights into the underlying changes in ecosystem functions, emergent properties, and robustness to extinction and invasion (Tylianakis et al. 2007; Tylianakis & Binzer 2013). These efforts have been hindered by the difficulty of quantifying variation among interaction networks. The challenge lies in finding a meaningful way to measure the dissimilarity between networks (Dale & Fortin 2010). Given the ecological properties or processes of interest, a direct comparison – not always computationally tractable – may not be necessary. Hence, networks can be indirectly compared through their properties (e.g., degree distribution, connectance, nestedness, modularity, etc.). Multivariate analyses of network metrics have been used to estimate the level of similarity between different networks (Vermaat et al. 2009; Baiser et al. 2012), while null models were used to compare observed values statistically to their expected random counterparts (e.g., Flores et al. 2011).

In the situation where several networks share a large enough number of species, one can alternatively compare how these shared species interact. This approach can be particularly useful along environmental gradients (Tylianakis et al. 2007; Tylianakis & Morris 2017). It represents a second 'dimension' of network variability, where in addition to changes in higher order structure, changes at the scale of species pairs within the networks are accounted for. This variation is more readily measured through a different approach to sampling, where instead of relying on the sampling of a large number of networks in different environments, efforts are focused on the same system at reduced spatial or temporal scales. The development of methods to analyse replicated networks is still hampered by the lack of such data; this is especially true in food webs. Replicated food webs based only on the knowledge of the local species and their potential interactions (e.g., Havens 1992) are not always appropriate: by assuming that interactions always happen everywhere, we do not capture all sources of community variation (in addition to the issue of co-occurrence being increasingly unlikely when the number of species increases). Sampling of ecological networks should focus on the replicated documentation of interactions within the same species pool, and their variation in time and space (Poisot et al. 2012; Carstensen et al. 2014; Olito & Fox 2015), as opposed to relying on proxies such as comparison of different communities across space (Dalsgaard et al. 2013), or time (Roopnarine & Angielczyk 2012; Yeakel et al. 2014).

Analysis of network structure measures has so far played a central role in the comparison of networks and in the search for general rules underpinning their organization (Dunne 2006; Fortuna et al. 2010). Notably, the number of species affects the number of interactions in real ecological networks (Martinez 1992; Brose et al. 2004), and thus many other network properties (Dunne 2006). Some measures of network structure covary with expected ecological properties, such as species abundance distributions (Blüthgen et al. 2008; Vázquez et al. 2012; Canard et al. 2014), network size and sampling intensity (Martinez et al. 1999; Banašek-Richter et al. 2004; Chacoff et al. 2012). This issue can seriously limit the interpretation of network measures and their use for network comparison. Furthermore, most of these measures are highly correlated among themselves: Vermaat et al. (2009) reported that network variation can be reduced largely along three major axes related to connectance, species richness (which is tied to connectance because the number of interactions scales with the number of species) and primary productivity (which is hard to measure, and is not easily defined for all systems). More recently, Poisot & Gravel (2014) and Chagnon (2015) showed that because of constraints introduced by the interaction between connectance and network size, the covariation of the simplest measures of network structure is expected to be very strong. As a consequence, it is barely possible to make robust network comparisons using the variations in these basic descriptors. We therefore need to go beyond these global network properties, and find meaningful alternatives that allow a better understanding of the ecological differences between networks.

Differences in global structure Other methods accounting for the structure of the entire network have been developed. For example, some methods are based on the frequency distribution of small subnetworks including network motifs (Milo 2002) and graphlets (a more general definition of motifs; Przulj 2007; Yavero lu et al. 2015). The method of graph edit distance gives edit costs (each modification to the graph counts for one unit of distance) for relabelling nodes, as well as insertion and deletion of both nodes and interactions (Sanfeliu & Fu 1983), and therefore provides a well-defined way of measuring the similarity of two networks (this method has not been widely used in ecology). Other suitable measures to determine network similarity are based on graph spectra (Wilson & Zhu 2008; Stumpf et al. 2012). Spectral graph theory (which is yet to be applied comprehensively to the study of species interaction networks, but see Lemos-Costa et al. (2015)) characterizes the structural properties of graphs using the eigenvectors and eigenvalues of the adjacency matrix or the closely related Laplacian matrix (the Laplacian matrix, defined as $\mathbf{D}-\mathbf{A}$, wherein $\mathbf{D}$ is a matrix filled with 0's in the off-diagonal elements, and the degree of each node is on the diagonal and accounts both for network structure and for degree distribution). Some methods allow the algorithmic comparison of multiple networks in which no species are found in common (Faust & Skvoretz 2002; Dale & Fortin 2010), and are primarily concerned with the overall statistical, as opposed to ecological, properties of networks.

Ecological similarity and pairwise differences All of the aforementioned methods are adapted from other fields (usually physics) and focus on networks as mathematical abstractions. Developing new methods, rooted in ecological processes, to compare ecological networks would potentially provide new important insights.@pois12dsi presented a framework for measurement of pairwise network dissimilarity, accounting both for species and interactions turnover through space, time or along environmental gradients. This method extends the notion ofβ-diversity to the network of interaction underlying communities Following Koleff et al. (2003), this approach partitions interactions in three sets: shared by both networks, unique to network 1, and unique to network 2. The β-diversity can be measured by comparing the number of interactions shared and unshared bythese three sets to reflect symmetry of change, gain/loss measures, nestedness of interaction turnover, etc. This method of network β-diversity can also be extended to multiple network comparisons using their relative difference from the same meta-network. While many measures of β-diversity exist to analyse compositional data, there is still a lack of a comprehensive methodology regarding their application to networks. A large part of this stems from the fact that species interactions require the species pair to be shared by both communities, and consequently some analyses require that the species pair is shared by two communities: measures of network β-diversity are strongly constrained by the structure of species co-occurrence. If no species pairs co-occur, or if no two networks have common species, these methods cannot give informative results (the dissimilarity being, by default, complete) – as of now, this suggests that a tighter integration of these methods with research on compositional turnover is needed, especially to understand the threshold of shared species below which they should not be applied. In addition, none of the current methods seem sufficient to characterize the structure for a meaningful comparison and to extract information hidden in the topology of networks (as they ignore network-level structure, i.e., emerging from more than direct interactions), and the development of future methods that work regardless of species composition seems like a straightforward high-priority topic. Finally, this framework would benefit from a better integration with quantitative measures. Using Bray-Curtis (or equivalent) measures to assess difference between networks for which interaction strengths are known would allow us to quantify dissimilarity beyond the presence or absence of interactions.

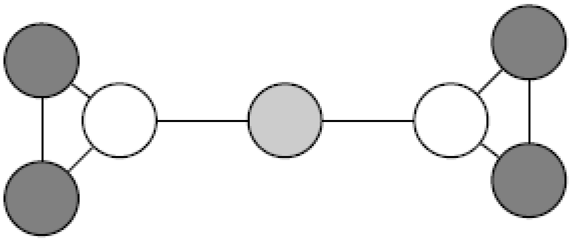
3.3.3 What do species do?

Not all species in large communities fulfill the same ecological role, or are equally important for processes and properties acting in these communities. As species interactions are a backbone for fundamental mechanisms such as transfer of information and biomass, one can expect that the role of a species reflects its position within its community, organized by trophic level, abundance, body size or other ecologically meaningful organizing principles. In species interaction networks, it is possible to measure the position and the role of species in different ways, giving different ecological information.

Centrality Centrality is a measure of how "influential" a species is, under various definitions of "influence". It has been used to identify possible keystone species in ecological networks (Jordán & Scheuring 2004; Martín González et al. 2010). We note that the ability of network structure measures to identify keystone species is highly dubious; the canonical definition of a keystone species (Paine 1969) requires knowledge about biomass and effects of removal, which are often not available for network data, and makes predictions that are primarily about species occurrences. These measures may be able to identify list of candidate keystone species, but this requires careful experimental/observational validation. Nevertheless, knowledge of network structure allows us to partition out the effect of every species in the network. For example, in networks with a nested structure, the core of generalist species have higher centrality scores, and the nested structure thought to play an important role for network functioning and robustness (Bascompte et al. 2003). We provide an illustration of some centrality measures in fig. 3.4.

Degree centrality ($C_D(i) = k_i$; Freeman (1977)) is a simple count of the number of interactions established by a species. In directed networks, this measure can be partitioned between in-degree (interactions from others to i) and out-degree (interaction from i to other). It is a local measure, that quantifies the immediate influence between nodes. As an example, in the case of a disease, a node with more interactions will be more likely both to be infected and to contaminate more individuals (Bell et al. 1999). To compare species' centrality, C_D has to be normalized by the maximum degree ($\langle C_D \rangle = C_D / k_{\text{max}}$).

Closeness centrality (C_C) (Freeman 1978; Freeman et al. 1979) measures the proximity of a species to all other species in the network, and is therefore global in that, although defined at the species level, it accounts for the structure of the entire network. It is based on the shortest path length between pairs of species and thus indicates how rapidly/efficiently a node is likely to influence the overall network. The node with the highest C_C is closer to all other nodes than



	Betw.	Eigen.	Degree	Close.
◍	**0.36**	0.15	0.12	**0.18**
●		0.13	0.12	0.12
○	0.32	**0.17**	**0.19**	0.17

Figure 3.4 On the simple graph depicted at the top (nodes of the same shade have the same centralities), we measured centrality using betweenness, eigen centrality, degree centrality, and closeness. The values have been corrected to sum to unity. The value in bold gives the most central family of nodes for the given measure. This example illustrates that different measures make different assumptions about what being "central" means. The dark-grey nodes do not have a betweenness centrality value; some software returns 0 for this situation.

any other nodes and will thus affect more rapidly the overall network if, for example, there is a perturbation (Estrada & Bodin 2008). Formally, C_C is defined as

$$C_C(i) = \sum_{j \neq i} \frac{n-1}{d_{ji}}\,, \tag{3.3}$$

where d_{ij} is the shortest path length between i and j, and n is the number of species.

Betweenness Centrality (C_B) (Freeman 1977) describes the number of times a species is between a pair of other species, i.e., how many paths (either directed or not) go through it. This measure is thus ideal to study the influence of species loss on fragmentation processes, for example (Earn 2000; Chadès et al. 2011; McDonald-Madden et al. 2016). Nodes with high C_B values are considered as module connectors in the network. The value of C_B is usually normalized by the number of pairs of species in the network excluding the species under focus, and is measured as

$$C_B(i) = 2 \times \sum_{j<k; i \neq j} \frac{g_{jk}(i)/g_{jk}}{(n-1)(n-2)}\,, \tag{3.4}$$

where g_{jk} is the number of paths between j and k, while $g_{jk}(i)$ is the number of these paths that include i.

Eigenvector centrality (C_E – Bonacich 1987) is akin to a simulation of flow across interactions, in which each species influences all of its partners simultaneously. It then measures the relative importance of species by assigning them a score on the basis that an interaction with more influential species contributes more to a species' score than the same interaction with a low-scoring species (Allesina & Pascual 2009b). From a graph adjacency matrix **A**, the eigenvector centrality of species i is given by

$$C_E(i) = \frac{1}{\lambda} \sum_{j} \mathbf{A}_{ij} C_E(j)\,, \tag{3.5}$$

where $\mathbf{A}_{ij}$ is 1 if i interacts with j and 0 otherwise, and λ is a constant. This can be rewritten as the eigenvector equation:

$$\mathbf{Ac} = \lambda \mathbf{c}\,, \tag{3.6}$$

wherein $\mathbf{c}$ is the vector of all values of C_E. As all values of C_E have to be positive, as per the Perron-Frobenius theorem, λ is the greatest eigenvalue of $\mathbf{A}$.

Finally, Katz's centrality (C_K – Katz 1953) is a measure of the influence of a node in the network. This measure takes into account all the interactions connecting a node to its neighbourhood. However, an immediate neighbour has more weight than a distant one. C_K is defined as

$$C_K(i) = \sum_{k=1}^{\infty} \sum_{j=1}^{n} \alpha^k \mathbf{A}_{ij}^k\,, \tag{3.7}$$

wherein α is the attenuation constant, and k is the length of the paths between i and j. The α value is between 0 and $1/\lambda$, where λ is the largest eigenvalue of $\mathbf{A}$. Larger values of α give more importance to distant connections, thus allowing this measure to function either locally (immediate neighborhood) or globally (entire graph). C_K can be used in directed acyclic graphs (e.g., trees), which is not true of C_E. This is also the only measure to have a probabilistic equivalent (Poisot et al. 2016a).

Studying different measures of centrality provides important information regarding the roles of certain species/nodes. As an example, a species may have a low C_D and a high C_B, meaning that it plays a key role in connecting species that would not be connected otherwise even if it does not interact with them directly. A low C_D and a high C_C means that the species has a key role by interacting with important species. Because the absolute values of centrality vary with network size and connectance, Freeman et al. (1979) suggested that the centralization measure, rarely applied in ecology, be used when comparing centrality across networks. Centralization is defined, for any centrality measure C_x, as the sum of the differences between each node's centrality, and the highest centrality value ($\sum_i (C_x(i) - \max(C_x))$). This measure is then divided by the maximal possible value of centralization for a network with the same number of nodes and interactions, which in turn depends on the formulae used to measure centrality, and can be estimated based on random draws of the networks.

Species roles in the network Species functional roles can be reflected in the interactions they establish (Coux et al. 2016), providing a clear bridge between network approaches and functional ecology studies. Functional traits are known to be correlated with the position of species in the network, either because they intervene directly in the interaction (Brose et al. 2006a; Alexander et al. 2013), constraining the set of possible interactions or their frequency, or because phenological incompatibilities prevent the interaction from happening (Olesen et al. 2011). For instance, (Petchey et al. 2008a) used allometric scaling of body size and foraging behaviour of individual consumers to predict species interactions. Scaling up to multiple traits, one can group species into functional clusters, based on their similarity. The distribution of some species-level network measures (e.g., centrality, degree) can then be compared within and across groups (Petchey & Gaston 2002). This method usually does not account directly for interactions between species (Petchey et al. 2008a) but is useful when studying a process for which the influential traits are known, or to test the importance of a particular (complex of) traits on a function. Moreover, when the trait used is correlated to diet choice (e.g., body mass), and because we know that networks are usually interval(see paragraph on intervality), this may group interacting species.Note that one can, in this situation, adopt a very generous definition of what constitutes a trait: spatial grouping of species (Baskerville et al. 2011) is one example in which examining interactions in the light of species attributes provides ecological insights.

If external information on species traits is absent, the role of a species can be approached through the interactions it establishes within the network: species with similar interactions are often grouped into trophic species, and these can be assumed to have similar traits or lifestyles (this approach has mostly been used in food webs). Indeed, many food-web models (Williams & Martinez 2000; Cattin et al. 2004) predict interactions between trophic groups, and not between species. Lumping species within trophic groups maintains the heterogeneity of interactions across groups, but removes all variability of interactions between species within the groups. As a consequence, species that bring unique interactions to a trophic group may be overlooked. Dalla Riva & Stouffer (2015) suggested an alternative to this approach: species positions are analysed before clustering them into groups (i.e., there is a measure of position for every species), allowing explicit investigation of species interactions while avoiding obfuscation of the variance within groups.

Coux et al. (2016) measured the functional role of species, by applying functional dispersion $FDis$ (Laliberté & Legendre 2010) to the adjacency or incidence matrix of the network. Under this framework, as in Mouillot et al. (2013), the uniqueness of a species is hinted at by its distance to the centroid of all other species. We argue that this approach should be questioned for two reasons. First, it is sensitive to the ordination choices made. Second, it is not clear how it allows the comparison of results across different networks: not only does the position of a species vary in relation to other species in the network, it varies from one network to another. Note that centrality measures are not necessarily better at identifying which species are unique: as we show in fig. 3.4, for some measures, non-unique nodes have high centrality values. We argue that the development of measures for node uniqueness should receive increased attention. In particular, measures that rely on ordination only account for first-order interactions, i.e., direct interactions between species. As a consequence, a large part of the network structure, which emerges through consideration of longer chains of interactions, is not accessible via these methods.

Looking at network motifs is a promising way to address species functional roles and node uniqueness. Motifs are all the possible ways a fixed number of species (usually three or four) can interact. Within these motifs, species can occupy a variety of unique positions; for example, within a linear food chain, there are three distinct positions (bottom, middle, top), whereas a trophic loop has a single unique position. Within motifs with three species, 30 unique positions can be identified (Stouffer et al. 2012), and for each species, its frequency of appearance at each of these positions within networks has been shown to be an inherent characteristic conserved through its evolutionary history. This method has the advantage of grouping species that may be different in terms of guild or partners, but that contribute in the same way to the structure of the community. Based on this vector it is possible to identify species statistically that exhibit similar profiles. Motif positions tend to be well conserved both in time (Stouffer et al. 2012) and space (Baker et al. 2014), making them ideal candidates to be investigated alongside functional traits and phylogenetic history.

Partition based on modularity In large communities, some species are organized in modules (see “What do communities look like” part “Edges repartition within the graph”), within which they interact more frequently among themselves than with species of the same overall network but outside of their module. Guimerà & Amaral (2005b) proposed that when functional or topological modules can be found in large networks, the functional role of a species can be defined by how its interactions are distributed within its module and with other modules. To identify these roles, the first step is to identify the functional modules of a large network (see “What do communities look like” part “Edges repartition within the network”). The profile of species interactions is determined by using two measures.

First, the *z*-score quantifies how well-connected a species *i* is within its module *m*.

$$z_i = \frac{K_i - \overline{K}_{m_i}}{\sigma_{K_{m_i}}}, \tag{3.8}$$

where K_i is the degree of *i* within its module m_i; $\overline{K}_{m_i}$ is the average of K over all species of m_i and $\sigma_{K_{m_i}}$ is the standard deviation of K in m_i.

Second, the participation coefficient (PC) describes the profile of *i*’s interaction with species found outside of the module m.

$$PC_i = \sum_{m=1}^{N_M} (\frac{K_{is}}{k_i})^2 \,, \tag{3.9}$$

where k_i is the total degree of species i, meaning a count of all its connections, inter- and intra module. The PC of a species therefore varies between 0 (all interactions are within the module) and 1 (all interactions are uniformly distributed among all modules). The use of these indices is based on the assumption that species with similar interactions have similar traits and so are expected to play the same functional role.

Olesen et al. (2007) used these two values to divide species into four groups, based on a cutoff for z (2.5) and for PC (0.62). Species with low z and low PC are "peripherals" – they are not well connected within or between modules. Species with low z and high PC connect well between, but not within, modules, and are "connectors". Species with high z and low PC are "module hubs", well connected within their own modules but not with the outside. Finally, species with high z and high PC are "network hubs", connecting the entire community. In their analysis of plants and pollinators, Olesen et al. (2007) revealed that pollinators tend not to be module hubs, and are also less frequently network hubs than plants are.

Contribution to network properties. As species make differential contributions to network structure and processes, the removal of certain species will therefore have a greater effect on the community's stability and functioning, and these species are therefore stronger contributors to these processes. Differential contribution to several processes can be estimated in multiple ways: by performing removal/addition experiments in real ecological systems (e.g., Cedar creek or BIODEPTH experiments), by analyzing the effect of a species extinction within empirical (Estrada & Bodin 2008) or simulated (Berlow et al. 2009) systems, by using a modelling approach and simulating extinctions (Memmott et al. 2007), or by analyzing the statistical correlation between an ecosystem property and species functional roles (Thompson et al.

2012). Another way to quantify the contribution of a species to a property P is to compare it to its contribution to the same property when its interactions are randomized (Bastolla et al. 2009). This method allows studying the contribution of a species' interactions, as the variation of interactions is intuitively expected to be faster than the variation of species. Indeed, because interactions require species to co-occur, because there are far more interactions than species, and because interactions have dynamics of their own, whether there will be more signal in interactions than in species presence is an hypothesis that should be tested on empirical systems in priority.

The contribution of a species to a given network measure after its interactions are randomized is

$$c_i = \frac{(P - \langle P_i^\star \rangle)}{\sigma_{P_i^\star}}\,, \tag{3.10}$$

where P is the property (nestedness, modularity, productivity, …), $\langle P_i^\star \rangle$ and $\sigma_{P_i^\star}$ are the average and standard deviation, respectively, of the property across a set of random replicates for which species i interactions have been randomized. The effects of several traits or structural properties of species (such as centrality or species trophic roles) on their contributions to given measure can then be analyzed.

3.3.4 How similar are species interactions?

Some species exhibit a much larger set of interactions than others or form denser clusters within the network. One of the many challenges of ecology is to understand the causes and consequences of such heterogeneous species interactions. Species are, first and foremost, related by their phylogenetic history. We will not address this aspect here, because it does not easily integrate with network theory. We encourage readers to refer to Cadotte & Davies (2016) instead.

One way in which the heterogeneity of species interactions is quantified is through analysis of the overlap in their partners, known as ecological similarity. For simplicity, we will use the vocabulary derived from trophic networks, but these methods can also be applied to other types of ecological networks. Ecological similarity between species is a widely used concept that quantifies the resemblance between two species or “biotic interaction milieu” (McGill et al. 2006) and allows analyzing processes ranging from species niche (Elton 1927) and community assembly (Piechnik et al. 2008; Morlon et al. 2014) to trophic diversity (Petchey & Gaston 2002). The simplest and most widely used measure of pairwise ecological similarity is the Jaccard coefficient (Legendre & Legendre 2012):

$$S_J = \frac{a}{a+b+c} \tag{3.11}$$

where a is the number of shared partners, b the number of species that interact with only the first species and c with only the second species (for variations, see (Legendre & Legendre 2012)). The Jaccard similarity coefficient is widely used to estimate ecological similarity and competition between species (Rezende et al. 2009) but does not account for the shared absence of interactions (but see Chao et al. 2005). This is not a severe issue, as ecological networks tend to be extremely sparse, and therefore shared absence of interactions may not be informative. The similarity index has to be chosen with care depending on the focus of the study. In the general equation above, consumers and resources are seen as perfectly equivalent (additively), but, in directed networks, it can be adapted to include consumer and resources as different dimensions of trophic activities and/or for dynamical food webs by including information about flows (Yodzis & Innes 1992). Once a similarity matrix is formed from all pairwise measurements, a hierarchical clustering can be performed to build a dendrogram, which gives information about the trophic diversity of species within a community and the relative uniqueness of species (but see Petchey et al. 2008b). Cophenetic correlation (Sokal & Rohlf 1962) can then be used to analyze how well several dendrograms, built using different methods, preserve the similarity between species (Yodzis & Winemiller 1999). The similarity of overall communities can also be estimated to see how similar, or dissimilar, species within it are when compared to null models (Morlon et al. 2014). For this purpose, the mean or maximum pairwise similarity is averaged across the whole network under consideration.

3.3.5 Is any of this significant?

Most network properties tend to be colinear (Vermaat et al. 2009), specifically because they covary with the number of species and links (MacDonald et al. 2020). For example, the number of interactions in a network with a known number of species will limit the possible values of nestedness, modularity, and so on (Poisot & Gravel 2014). As such, the value of any measure of network structure often needs to be compared to a range of possible values under a null model. The purpose of the null model is to search the null space of possible randomized networks (Fortuna et al. 2010), in a way that would yield an unbiased distribution of the measure of interest, to which the observed value is then compared. In practice, this approach is constrained by (i) the size of the null space to search, and specifically the fact that it varies with connectance (Poisot & Gravel 2014), and (ii) the computational burden of a thorough null space exploration.

A large number of studies use the null hypothesis significance testing (NHST) paradigm to assess the significance of an observed value of network structure. NHST works by generating randomized networks under a variety of constraints, measuring the property of interest on these randomizations, then commonly using a one-sample *t*-test with the value of the empirical measure as its reference. This is justified because, through the mean value theorem, the application of enough randomizations should yield a normal distribution of the simulated network measure (see Flores et al. 2011). Bascompte et al. (2003) used a probabilistic sampling approach, where the probability of drawing an interaction depends on the relative degree of the species; Fortuna & Bascompte (2006) used the same approach, with the distinction that all interactions have the same probability (equal to connectance). Drawing from a probability distribution in this manner has a number of shortcomings, notably the fact that some species can end up having no interactions, thus changing the network size (which Fortuna et al. 2010 termed "degenerate matrices"). An alternative approach is to use constrained permutations, where pairs of interactions are swapped to keep some quantity (the overall number of interactions, the degree of all species, and so on) constant. This approach is used in null models for species occupancy (Gotelli 2000; Gotelli & Entsminger 2003; Ulrich & Gotelli 2007). Stouffer et al. (2007) used an intermediate approach, where swapping was done as part as a "simulated annealing routine", to give the algorithm enough leeway to explore non-optimal solutions before converging (as opposed to just swapping, which has no definition of the optimality of a solution). Another possibility is to use alternatives to null model testing, as proposed by@macd20rls. Seeing that the number of links may be best viewed not as a fixed but rather a probabilistic quantity (Poisot et al. 2016a), they suggest using mathematical models instead of simulation of random matrices to provide a domain of expected values. This type of alternative methods, as null models, requires more development.As of now, there are no clear recommendations as to which approach to sample the null space is the most efficient (or computationally feasible for large network sets), emphasizing the need for a more exhaustive comparison of the behaviour of these methods.

Hypotheses underpinning null models The most frequently used null models are topological, i.e., they can search the null space based only on the matrix, and do not rely on ecological processes to generate random networks. We will focus on the subset of null models which generate a probability of observing an interaction based on different aspects of network structure; these probabilistic networks can be analysed directly or, as is most commonly done, converted into binary networks through random draws. There are three broad categories of null models (commonly used for bipartite networks) – based on connectance, based on degree distribution, and based on marginal degree distribution. Each family embodies a specific hypothesis about the sources of bias on the measured property. Type I (Fortuna & Bascompte

2006) null models are focused on connectance, where the probability of any two species i and j interacting is fixed as

$$P_{i\to j} = \frac{|E|}{|T| \times |B|}\,, \tag{3.12}$$

where T and B are nodes from the "top" ($T = \{v \in V, k_{\text{in}}(v) = 0\}$) and "bottom" ($B = \{v \in V, k_{\text{out}}(v) = 0\}$) levels of the network (these methods were originally applied to bipartite networks). This model assumes that interactions are distributed at random between all species, without considering the degree of the species. Deviation from the predictions of this model indicate that the network measure of interest cannot be predicted by connectance alone.

Type II null models (Bascompte et al. 2003) add an additional level of constraint, in that they respect the degree distribution of the network (in degree k_{in} ; out-degree k_{out}). In a Type II network,

$$P_{i\to j} = \frac{1}{2}\left(\frac{k_{\text{in}}(j)}{|T|} + \frac{k_{\text{out}}(i)}{|B|}\right)\,, \tag{3.13}$$

meaning that the interaction is assigned under the hypothesis that i distributes its outgoing interactions at random, and j receives its incoming interactions at random as well. In this model, species with more interactions have a higher probability of receiving interactions in the simulated network. This conserves both the distribution of generality and vulnerability. Deviation from the predictions of this model indicate that the network measure of interest cannot be predicted by the degree distribution alone.

Finally, Type III models account for only one side of the degree distribution, and can be defined as Type III in, wherein

$$P_{i\to j} = \frac{k_{\text{in}}(j)}{|T|}\,, \tag{3.14}$$

and Type III out, wherein

$$P_{i\to j} = \frac{k_{\text{out}}(i)}{|B|}\,. \tag{3.15}$$

Deviation from the predictions of this model indicate that the network measure of interest cannot be predicted by the marginal degree distributions alone. Ecologically speaking, deviation from this null model means that the way interactions are established/received is sufficient to explain the observed structure. These models can be expressed in a sort of hierarchy. Type I introduces the least hypotheses, and should be applied first. If there is no significant deviation, then Type III models can be applied, then Type II. This approach has the important benefit of, in addition to determining which properties show a difference from the random expectation, giving insights about which aspect of the structure are responsible for this difference.

Topological and generative models It is important to note that these models, based on permutations, are purely topological. There is no difference, when deciding if an interaction should be assigned between two species, between e.g., a plant-pollinator network, or a host-parasite network. One may want to test deviation from a null distribution that would be informed by ecological processes. To inject some processes into the null models used, several "generative" models have been proposed. In contrast to topological models, generative models use core assumptions about ecological mechanisms to generate networks that mimic aspects of a template network. Arguably the most influential (despite it being limited to trophic interactions) is the "niche model" (Williams & Martinez 2000), that generates networks of trophic groups based on the hypothesis that feeding interactions are determined by an arbitrary niche-forming axis generally accepted or implied to be body-size ratios (Brose et al. 2006a). Gravel et al. (2013) showed that the parameters of this model can be derived from empirical observations. The niche model assumes a beta distribution of fundamental niche breadth in the entire network (in cases where the trait space is bound between 0 and 1); this assumption, close though it may be to empirical data, nevertheless has no mechanistic or theoretical support behind it. This suggests that so-called generative models may or may not be adequately grounded in ecological mechanisms, which implies the need for additional developments. Similar models include the cascade model and the nested-hierarchy model, but these tend to generate networks that are qualitatively similar to those of the niche model (Brose et al. 2006b). More recently, several models suggested that species traits can be used to approximate the structure of networks (Santamaría & Rodríguez-Gironés 2007; Bartomeus 2013; Crea et al. 2015; Olito & Fox 2015; Bartomeus et al. 2016). Finally, networks tend to be well described only by the structure of species abundances. Both in food webs (Canard et al. 2012) and host-parasite bipartite networks (Canard et al. 2014), modelling the probability of an interaction as the product of relative abundance appears sufficient to generate realistic networks. These generative models represent an invaluable tool, in that they allow building on mechanisms (although, as we illustrate with the niche model, not necessarily ecological ones) instead of observed relationships to generate the random expectations. The NHST-based analyses then proceed as with topological models, i.e., the observed value is compared to the distribution of values in the theoretical space.

3.3.6 Future methods for novel questions

Surveying the methodological toolkit available to analyze ecological networks highlights areas in which future developments are needed. We identified, in particular, four topics that require additional attention.

Multi/hyper graphs Most of the tools to analyse species interaction networks are limited to node-to-node interactions, to the exclusion of node-to-interaction or interaction-to-interaction interactions. This limits the variety of biological situations that can be represented. Golubski & Abrams (2011) presented a number of situations that elude description in this way. For example, opportunistic infection by a pathogen O requires the pre-existence of an interaction between a pathogen P and an host H. This situation is better captured as (i) the existence of an interaction between H and P (noted L_{HP}) and (ii) the existence of an interaction between O and this interaction, noted $O \to L_{HP}$. Another hard-to-represent scenario is niche pre-emption: if a host H can be infected by either pathogen P_1 or P_2, but not both at the same time, then the interactions L_{HP_1} and L_{HP_2} interact antagonistically. This is a different situation from simple competition between P_1 and P_2. Although these are extremely important drivers of, for example, species distributions (Araújo & Rozenfeld 2014; Blois et al. 2014), the current methodological framework of ecological network analysis is not well prepared to represent these data.

External information Building on the basis suggested by Poisot et al. (2015c), Bartomeus et al. (2016) proposed that the mechanisms determining ecological interactions can be identified within a cohesive statistical framework, regardless of the type of ecological interaction. At its core, their framework assumes that interactions are the consequence of matching rules, i.e., relationships between trait values and distributions. For example, a pollinator can get access to nectar if its proboscis is of a length compatible with the depth of the flower. Rather than relying on natural history, these "linkage rules" (Bartomeus 2013) can be uncovered statistically, by modelling an interaction L_{ij} as a function $f(x_i, y_j)$ of the traits involved, wherein x_i and y_j are sets of traits for species i and j respectively. Procedures akin to variable selection will identify the traits involved in the interaction, and model selection can identify the shape of the relationship between trait values and interactions. There are two reasons for which this work is an important milestone in the modern analysis of ecological networks. First, it places interactions within the context of community ecology, by showing how they build upon, and influence, trait distributions. In particular, it draws attention to how structure of networks results both from the linkage rules and from the distribution of traits in the locality where the network is measured (Gravel et al. 2016a). Second, it does away with the necessity of topological models to generate random networks: identifying matching rules is the only step needed to generate random networks based on functional, biological hypotheses, thereby solving some of the concerns we identified with generative null models. We argue that this approach should be expanded to accommodate, e.g., phylogenetic relationships among species. The ideal framework to study networks, and the one we should strive for, avoids considering interactions in isolation from other aspects of community structure – instead, it is explicit about the fact that none of these aspects are independent. Although this will come with additional mathematical and statistical complexity, this cost will be more than offset by the quality and the refinement of the predictions we will make.

Although documenting species, traits, and interactions seems like a daunting effort, there are novel approaches to accelerate the generation of data in some systems. For example, Bahlai & Landis (2016) showed that passive measurement based on citizen science (using Google Images) allows users to accurately document phenological matches and species interactions between flowers and bumblebees. Similarly, Evans et al. (2016) showed that sequencing of diet gives access to phylogenetic and interaction history within a single experiment. Addressing novel questions will require a diversification of the methodological toolkit of network ecologists, as well as an improved dialogue between empiricists and theoreticians.

Networks of networks An additional frontier for methodological development has to do with the fact that networks can be nested. A network of species–species interactions is the addition of interactions at the population level (Poisot et al. 2015c), themselves being aggregates of interactions at the individual level (Dupont et al. 2011, 2014; Melián et al. 2014). This is also true when moving from single-site to multi-site network analysis (Poisot et al. 2012; Canard et al. 2014; Carstensen et al. 2014; Trøjelsgaard et al. 2015). Local interaction networks exist in meta-community landscape (Gravel et al. 2011; Trøjelsgaard & Olesen 2016), and their structure both locally and globally, is constrained by, but is also a constraint on, co-occurrence (Araújo et al. 2011; Cazelles et al. 2015).

Analyzing networks in a meta-community context might require a new representation. Most of this challenge comes from two sources. First, species are shared across locations; this means that two nodes in two networks may actually represent the same species. Second, networks are connected by species movement. Both the dynamics and the structure of networks are impacted by the fact that species move across the landscape at different rates and in different ways. The implication is that every species in the landscape potentially experiences its own version of the metacommunity (Olesen et al. 2010). Investigating community structure and the emerging dynamic processes in light of space would allow a more potent examination of the spatial structure and dynamics of ecological networks (Gouhier et al. 2010; Gravel et al. 2016b; Trøjelsgaard & Olesen 2016).

3.4 Managing species interactions networks data

The above analyses benefit from access to (context-enhanced) data on ecological interactions. An important point to raise is that the format expected for the analysis (i.e., when data are actively being processed) is different from the format suitable for storage, archival, mining, and linking. From an information management perspective, this places the question of What are ecological networks? in a new light.

Most of the measures mentioned above, and therefore most software, expect networks to be represented as matrices; every row/column of the matrix is an object, and the value at row *i* and column *j* is a measure of the interaction between *i* and *j*. It can be a Boolean value, a measure of interaction strength, or a probability of interaction. This approach is used by databases such as IWDB, Web-of-Life.es, and World of Webs (Thompson et al. 2012). Although this approach has the benefit of being immediately useful, it lacks the easy homogeneousaddition of metadata. In the context of species interaction networks, metadata is required at several levels: nodes (species, individuals), interactions, but also the overall network itself (date of collection, site environmental data, and so on). Most research has so far been constrained to the adjacency matrix representation of networks. However, ontologically richer representations (graphs with built-in metadata) may offer themselves to a larger and different tool set: multi-graphs, and hyper-graphs, capture a wider picture of ecosystems where all types of interactions are considered simultaneously. Food webs, or other networks, stored as binary or weighted matrices may not be the most relevant representation for these questions.

There are two initiatives that remedy this shortcoming by providing meta-data-rich information on ecological interactions. `Globi` (Poelen et al. 2014) is a database of interactions, extracted from the literature, and available through GBIF. It relies on an ontology of interaction types, and on unique taxonomic identifiers for species. `Mangal.io` (Poisot et al. 2015a) is a database of networks, that can be fed and queried openly through several packages; it relies on a custom data format, and can be linked to other databases through the use of taxonomic identifiers.

Networks formatted as raw matrices may well be immediately usable, but supplementing them with external information is hard. On the other hand, granular databases with rich metadata can always be converted to raw matrices, while retaining additional information. It is important that we maintain a distinction between the formats used for storage (in which case, relational databases are the clear winner) and the formats used for analysis (that can be generated from queries of databases). In order to facilitate synthesis, and draw on existing data sources, it seems important that the practice of depositing interaction matrices be retired, with the profit of contributing to the growth of context-rich databases. here are a handful of software packages available for ecological network analysis (Csardi & Nepusz 2006; Dormann et al. 2008; Hagberg et al. 2008; Hudson et al. 2013; Flores et al. 2016; Poisot et al. 2016a). They differ in their language of implementation, license, and methods availability.

Considerations about the analysis of networks go hand in hand with the far more difficult question of data sources and data quality. (Jordano 2016) showed that obtaining estimates of the completeness of sampling is both difficult, and different between weighted and unweighted networks. Describing the data at the level of the interaction in more detail may therefore give better estimates of (i) the robustness of the overall network, and (ii) the relevant aspects of life history to add in models. These can then be added to predictive models, in the form of functional traits (Bartomeus 2013; Bartomeus et al. 2016), to boost our ability to infer the existence of interactions (or their strength). Relevant interaction-level data (discussed in Poisot et al. 2015a) include the identity of species involved, their abundances, local environmental conditions, and functional traits of the individuals or populations observed interacting, when available. Shifting the focus of sampling away from networks, and onto interactions (because what are networks, but a collection of interactions?) would give more information to work with. Because the amount, resolution, and type of information that it is necessary and feasible to sample will vary for each system, empirical network scientists should lead the effort involved with developing data standards. Taking a step back, data quality should be framed within the context of a specific analysis; we feel that there is a need for a review that would attempt to determine the minimal amount of information needed as a function of the type of analyses that will be applied.

3.5 Conclusions

In this contribution, we have attempted a summary of the measures from graph theory that are the most frequently used in, or the most relevant to, the analysis of species interaction networks.

Even though species interaction networks are ubiquitous in community ecology, biogeography, macroecology, and so on, there is no clear consensus on how to analyse them. We identified a number of areas that would benefit from methodological development. We highlight each of these below, and identify whether they should stimulate future development of novel methods to complete the framework, or stimulate further investigation and assessment of existing methods to clarify when they should be applied.

There is a pressing need to accommodate hypergraphs and multigraphs within the network analysis framework, to allow work on a larger and more realistic variety of ecological situations. Pilosof et al. (2015) identified these systems as having a high relevance when predicting community change, and the emergence of zoonotic diseases, and this is a clear example of an area in which ecology and applied mathematics can have fruitful interaction.

The information we use in the building of network needs to be expanded. Far from being a collection of species and their interactions, networks are structured by environmental forces, species trait distribution, species evolutionary history, and random chance. Replicated data sets with extensive metadata and additional information would most likely boost our power to describe, explain, and predict network structure (Poisot et al. 2016b). The next generation of network measures should account for additional information carried by both species and interactions.

Of course, the addition of data to ecological interactions requires to expand the scope of what is currently being sampled, and to normalize it to some extent. More broadly, we expect that the development of novel methods, and the collection of novel data and their standardization, should go hand in hand. The emergence of interactions and networks databases, based around documented formats, is a step in the right direction, as they provide an idea of the scope of data to collect.

We need to establish stronger standards for the manipulation of network data. Networks are difficult to manipulate, and the lack of a robust software suite to analyse them is a very worrying trend – our knowledge of ecological networks is only as good as our implementation of the analyses, and academic code can always be made more robust, especially in fields where the widespread adoption of computational approaches is still ongoing. We expect that, since there are numerous initiatives to increase good practices in software engineering among academics, this problem will be solved by improved community standards in the coming years.

The NHST approach to network structure needs additional study, especially when it comes to determining best practice. Recent developments in graph theory, and notably edge-sampling based cross-validation (Li et al. 2020), can help assess the performance of generative null models. There is a shortage of null models that are based on topology but still account for known biology of the networks (such as forbidden interactions), highlighting the need for future developments.

There is a need to compare the alternative measures of a single property. We tried as far as possible to frame these measures in the context of their ecological meaning. But this can only be done properly by strengthening the ties between network analysis and field- or laboratory-based community ecology. Statistical analysis of measures on existing data sets will only go so far, and we call for the next generation of studies aiming to understand the properties of network structure to be built around collaboration between empirical researchers and measures developers.

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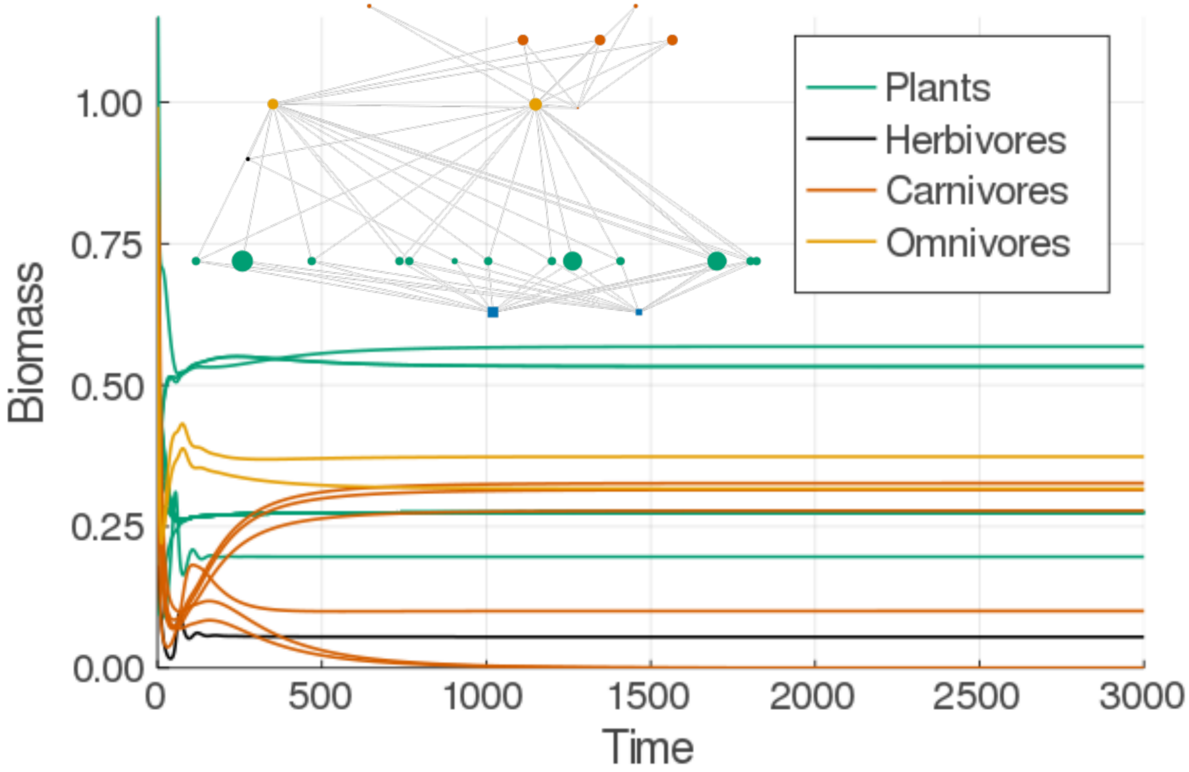
Chapter 4

Food web structure alters ecological communities top heaviness with little effect on the biodiversity-functioning relationship



Food web structure alters ecological communities top heaviness with little effect on the biodiversity-functioning relationship

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Abstract

In a rapidly changing world, the composition, diversity and structure of ecological communities face many threats. Biodiversity-Ecosystem Functioning (BEF) and community food-chain analyses have focused on investigating the consequences of these changes on ecosystem processes and the resulting functions. These conceptual frameworks have up to recently been often diverging, but each produced important results and identified a set of important mechanisms, that shape ecosystem functions. However, the frequent disconnectionbetween these frameworks, and the various simplifications of the study systems are not representative of the complexity of real-world communities. Here we use food webs as a more realistic depiction of communities, and use a bioenergetic model to simulate their biomass dynamics and quantify the resulting flows and stocks of biomass. We use tools from food web analysis to investigate how the predictions from BEF and food-chain analyses fit together, how they correlate with food-web structure and how it might help us understand the interplay between various drivers of ecosystem functioning. We show that food web structure is correlated to the community's efficiency in storing the captured biomass, which may explain the distribution of biomass (top heaviness) across the different trophic compartments (producers, primary and secondary consumers). While we know that ecological network structure is important in shaping ecosystem dynamics, identifying structural attributes important in shaping ecosystem processes and synthesizing how it affects various underpinning mechanisms may help prioritize key conservation targets to protect not only biodiversity but also its structure and the resulting services.

4.1 Introduction

Understanding the consequence of diversity on ecosystems process rates has become a pressing issueas we realized that human activities threaten both species existence (MEA 2005) and interactions (Poisot et al. 2015c) at a global scale. A variety of analyses have been conducted to investigate this particular problematic, and have produced important results (Tilman et al. 2014; Plas 2019) but the divide between them in concepts and approaches has hindered our ability to synthesize their results to build a general theoretical framework (Raffaelli 2006; Duffy et al. 2007; Hines et al. 2019).

In particular, while some studieshave focused on understanding the effect of “horizontal diversity” on ecosystems process rates (Biodiversity-Ecosystem functioning analyses or BEF) mainlythrough mechanisms derived from competition (Loreau & Hector 2001; Tilman et al. 2014), conversely others have focused on the effect of “vertical diversity” by aggregating species into trophic compartments along the food chain and using the concepts from food-chain theory (Fretwell 1987; Duffy et al. 2007; Loreau 2010a). Both approaches have produced important results, such as the paradigmatic BEF relationship (Tilman et al. 1996), or the consequences of trophic cascades on community structure (Paine 1980; Polis & Strong 1996; Borer et al. 2006; Gruner et al. 2008); but to build a mechanistic understanding of diversity effects on ecosystem process rates in natural communities, comprising many species along the food chain, we need to be able to reconcile both dimensions of diversity, as well as the different approaches used to study their effect in a single framework (Ives et al. 2005; Duffy et al. 2007; Thompson et al. 2012).

Recent efforts towards this goal have generally used dynamic consumer-resource models applied to food webs (Poisot et al. 2013; Schneider et al. 2016; Wang & Brose 2017; Wang et al. 2019; Buzhdygan et al. 2020). Studying the flux of biomass in ecological communities represented as their underlying network of trophic interaction – a map of whom eats whom, or food web – provide a powerful framework to investigate community functioning (Pascual & Dunne 2006; Thompson et al. 2012). We define functions here as the emerging rates and stocks of biomass transfers in food webs.Fluxes of nutrients and energy (commonly measured usingbiomass) in ecosystems represent the fundamental ecosystem process sustaining organisms, allowing their growth, underlying interaction between them and ultimately constraining the persistence and structure of the community (Barnes et al. 2018). As such, biomass fluxes represent a useful common currency to analyze, model and ultimately gain understanding of the aggregated ecosystem processes they underlay, from primary production to pressure of top carnivores (DeAngelis 1992), providing a way to estimate ecosystem multi-functionality (defined as the provisioning of multiple ecosystem functions; Barnes et al. 2018) and the potential to sustain various ecosystem services (Soliveres et al. 2016). By mapping trophic interactions, food webs also map biomass routes through the communities, the dynamics of the transfer of biomass through these routes can be modelled using adapted consumer-resource models such as Yodzis & Innes (1992). In parallel, the structure of these routes can be analyzed through a set of measures, adapted from graph theory, that carry a diversity of ecological information such as species degree of specialization, distance to producers, etc. (Dunne 2006; Delmas et al. 2019a). Characterizing the biomass distribution in food webs can also bring useful information. This results in an ideal framework for modelling communities functioning, and identifying its drivers.

First results from theoretical analyses of the BEF relationship in food webs show that the positive - hitherto paradigmatic - relationship between the diversity of species in a community and functioning rates appears to be dependent on the structure of the network (Thébault & Loreau 2006). For example, networks containing few VS. many generalist species would have qualitatively different BEF relationships. More recent in-silico experiments that followed have usually framed their analyses in more realistic communities, i.e., containing more species and using models that generate food webs with realistic structures of interactions (such as the niche model; Williams & Martinez 2000). The results of these studies show that the dependence on structure of the BEF relationship may not be as strong as previously thought, there still seems to be a positive relationship between diversity and functioning rates (Schneider et al. 2016; Wang & Brose 2017; Wang et al. 2019), but this relationship is relatively noisy. These studies, along with other more theoretical work (Poisot et al. 2013), have offered mechanisms that could extend the action of selection and complementarity to a framework involving competition and consumption, but no consensus has yet been reached.

Most of these recent analyses, using food webs to investigate diversity effects, although they integrate both dimensions of diversity (vertical and horizontal), do not necessarily attempt to bridge the gap between the conceptual frameworks that have emerged from the analysis of their effects in isolation (namely BEF and trophic chain theories). The analysis of trophic chains dynamics in particular has produced important results for understanding the functioning of ecosystems (Ives et al. 2005). Among these results is the fact that changes in richness (and thus the functioning of a trophic level since the BEF relationship is valid within the different compartments; Cardinale et al. 2006a) are reflected, via the trophic cascade, on all the other trophic levels (Duffy et al. 2007). In parallel the same kind of approach shows that the type of trophic interaction can also vary the strength of the trophic cascade. For example, depending on the proportion of omnivores (or intra-guild predators) in a community, a variation in consumer richness will not have the same impact on plant biomass (losing a predator leads to a reduction in plant richness, whereas a decrease in the richness of omnivores leads to an increase in their biomass; Polis & Strong (1996)).

One important results from food chain theory, and more specifically from analyzing the effect of community-level trophic cascades (as opposed as species-level; Polis 1999), is the influence on community shapes. By shape we refer to what is generally called trophic structure, i.e., a qualification of the distribution of biomass or abundance along the different trophic levels of the community (cascade or pyramid, top or bottom heavy). We use the term shape here to avoid confusion with the food-web network structure. The biomass distribution that characterizes trophic chains (and by extension networks) captures the synergy between dynamic, energetic and structural constraints shaping biomass transfers and underly community emerging functions (Barbier & Loreau 2019). Recent studies by Barbier & Loreau (2019) and Galiana et al. (2020) present a framework to reconcile predictions resulting from the use of different approaches in the study of food chains (energetic vs. dynamic). Their results show that community shape can theoretically inform us on the strength and direction of trophic control (what they call donor control vs. antagonistic feedback). While these results are still theoretical, we know that top-heavy (TH) and bottom-heavy (BH) food webs for example do emerge under different energetic constrains reflecting different internal dynamic processes (Leroux & Loreau 2008; McCauley et al. 2018; Woodson et al. 2018). Similarly pyramidal or cascade shapes could also be a reflection of other energetic or dynamic constraints (Barbier & Loreau 2019; Galiana et al. 2020).

We believe that investigating the link between the structure of interactions within food webs and food webs characteristic biomass distributions can help us identify the key mechanisms driving community functions. We also argue that the results of this analysis will help us understand the emergence if BEF relationships in food webs, as it captures the same energetic constraints.We expect for example that BEF relationships will be different depending on community shape, reflecting different energetic constraints on the dynamic transfers of biomass through trophic interactions. To test our hypothesis, we used food webs to represent communities, and simulated their biomass dynamics using a consumer-resource bioenergetic model adapted to food webs (Yodzis & Innes 1992; Williams et al. 2007). We investigated the potential link between the emerging shape of the communities, their food-web structure and BEF relationship. If our hypothesis proves to be valid, this would offer a possible explanation for the apparent idiosyncrasy of the BEF relationship in food webs. It would also provide ideas about the possible mechanisms responsible for the diversity-functioning relationship in complex ecological communities.

4.2 Methods

4.2.1 Biomass dynamics

To estimate biomass dynamics in food webs, we used a well-established bioenergetic food-web model (BEFWm). This model is an extension of Yodzis & Innes (1992) consumer-resource model to multiple resources and consumers (Williams et al. 2007). Biomass dynamics in this model hinge on three main dynamic processes described in the driving eq. 4.1 below: autotrophic production (first term of eq. 4.1), transfer of biomass through consumption (second and third terms of eq. 4.1), and loss of biomass because of metabolism (fourth term of eq. 4.1) and imperfect assimilation (e_{ji}). The details of the model for plant growth ($G_i(N)$), functional response (F_{ji}) and all parameter values are described in supplementary material (appendix 1, section S1).

$$B_i' = r_i G_i(N) B_i - \sum_{\text{j = consumers}} \frac{x_j y_j B_j F_{\mathrm{ji}}}{e_{\mathrm{ji}}} + \sum_{\text{k = resources}} x_i y_i B_i F_{\mathrm{ik}} - x_i B_i \tag{4.1}$$

Plant growth through autotrophic production is the basic process that sustains communities. Competition between plants for abiotic resources is a fundamental process of ecosystem functioning (Loreau et al. 2001; Cardinale et al. 2006b). We made this competition explicit by combining a well established (Tilman 1982; Huisman & Weissing 1999) and empirically tested (Passarge et al. 2006) model of nutrient intake for producers with a food-web consumer-resource model (following Brose 2008). The resulting bioenergetic model integrates the basic mechanism from which BEF relationships emerge – competition – with mechanisms that result from consumption (e.g., transfer efficiency). This approach yields more realistic results with fewer extinctions than classical consumer-resource models (Brose 2008), as it integrates feedback between bottom-up transfer of biomass from plants to consumers and top-down control of plant biomass by consumers.

In the nutrient intake model (Brose et al. 2005b, 2005a; Brose 2008), all producers share two nutrients N_1 and N_2. Nutrients availability is determined by their respective rates of supply, turnover and consumption by plants. Plants all have different half-saturation density for both nutrients, which results in a hierarchy of competition between them, as a lower half-saturation means a higher intake efficiency. As plants do not need all nutrients in the same quantities, we set nutrient content in plants (c_1 and c_2 for respectively N_1 and N_2) to reflect this. We set $c_1 = 1$ and $c_2 = 0.5$, meaning that plants need a higher quantity of N_1 than N_2. The half-saturation for N_1 is thus the primary driver of plants competitive hierarchy. The model equations are described in supplementary material (appendix 1, section S1.1.1).

Biomass is transferred through trophic interactions according to a multi-species functional response (Williams et al. 2007). This extension of the classical functional response accounts for consumers (resources) having multiple resources (consumers) and therefore accounts for both apparent and exploitative competition. We chose to implement a Holling type III functional response (Holling 1959; Real 1977) with homogeneous consumption among a consumer's resources, this allows us to have more stable systems, retaining more species (Brose et al. 2006b) and does not qualitatively change the results (Brose et al. 2006b; Schneider et al. 2012). Finally, biomass is lost through metabolism and imperfect assimilation. The functional response and its parameters are described in supplementary material (appendix 1, section S1.1.2).

The biological rates controlling these processes – namely the growth, maximum consumption and metabolic rates – are all dependant of two things: species metabolic class (vertebrate or invertebrate) and typical adult body size. In other words, we have an allometric scaling of biological rates with body size, with different allometric coefficient depending on the metabolic class.

4.2.2 Generating realistic food webs

We generated food webs with realistic structural properties using the Allometric Diet Breadth Model (ADBM, Petchey et al. 2008a). This model is based on optimal foraging theory and the allometry of foraging variables with body size. As such, it needs to be initialized with a vector containing species typical adult body sizes. It predicts realistic interactions from empirical food webs (Petchey et al. 2008a; but see Allesina 2011), and important food webs structural properties such as diet breadth and food web connectance, two potentially strong drivers of biomass dynamics.

To predict interactions between species, the ADBM model works in two steps. First it calculates the profitability (P_{ij}, or rate of energy intake) for each pair of species in the community. Then, it selects the links that maximize it. Profitability is expressed as a function of the net energy gained through trophic interactions (which scales linearly with the consumer body size), the encounter rate (which depends on the density of the resource species here expressed as biomass and the allometrically scaled attack rate) and the handling time. We chose to implement the "ratio" method for estimating handling time as it is supposed to yield more accurate results (Petchey et al. 2008a). In this formulation, handling time is estimated differently depending on the body-size ratio between a consumer and its potential resource. If the size difference is too big (bigger than a chosen threshold; see section S2) then we assume that the focus consumer is not able to consume the focus resource. See section S2 and Petchey et al. (2008a) for more detail on the model's equations and parameter values.

4.2.3 Numerical experiments

In order to generate realistic food webs that still express a generate wide range of richness and structure, we initialized the ADBM model with body-mass data from an empirical community: the Benguela pelagic community [Yodzis (1998); Brose et al. (2016); tab. S3 in appendix 1, supplementary material]. We chose this particular community because of the ability of the

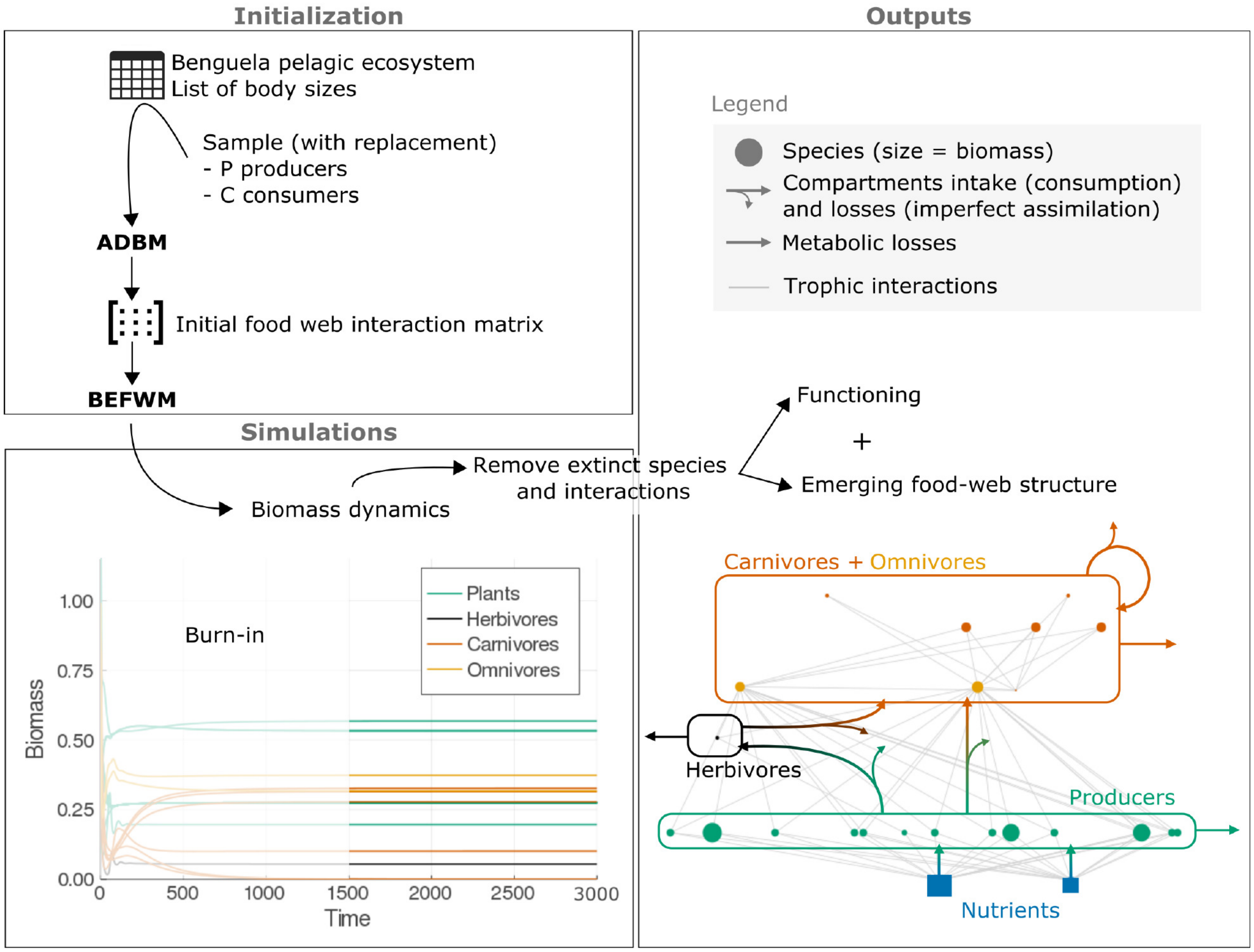


Figure 4.1 Conceptual representation of our experiments. Initialization (top left). We start by generating food webs with different levels of producer and consumer richness by sampling P producers and C consumers in a list of species (Benguela ecosystem as described in Yodzis, 1998). We retrieve the species body masses and metabolic classes. We pass the body masses to the Allometric Diet Breadth Model (ADBM, Petchey et al., 2008) to generate realistic food web interaction matrices. Simulation (bottom left). These matrices are passed to the Bioenergetic Food-Web model (Yodzis & Inès, 1992) to simulate their biomass dynamics. All species that have an average biomass below 10^{-6} during the second half of the simulation are considered as extinct, all interactions from and to them are removed. Outputs (right side). Emerging food-web structures, total biomasses and fluxes are calculated at the species level over the second half of the simulations and aggregated by trophic compartments (carnivores and omnivores in respectively dark and light orange, herbivores in black, producers in green). The whole system depends on the two basal nutrients (blue) that are shared by all producers (half-saturation densities for both nutrients are sampled and generate a hierarchy of competition). Nutrient supply at each time step is fixed throughout the simulations.

ADBM model to reproduce it quite well (Petchey et al. 2008a). We sampled species from those present in this community and recorded their body mass and metabolic class (vertebrate or invertebrate). The body masses were used to generate food-web interaction matrices (see fig. 4.1, top left panel), and metabolic classes were also used to calculate biological rates later used for the biomass dynamics simulations.

We generated food webs with 10 levels of producers richness (from 2 to 20), and 7 levels of consumer richness (from 5 to 35). For each of these 70 combinations of total species richness (7 to 55), we randomly generated up to 100 different food webs with the ADBM model. For each food web, we randomly drew the producers half-saturation density for the two shared nutrients, to generate a random hierarchy of competition among the different food webs. This design produces food webs with different richness, structure and ability to extract nutrients.

Because we wanted to set different typical consumer-resource body-mass ratio to explore the effect of allometric scaling, we did not use the original sampled body mass (used to generate food webs) in the simulations to calculate biological rates but reassigned body masses based on a sampled consumer-resource body-mass ratio (Z). A species i body mass (M_i) is calculated from Z and its trophic level (t_i) in the following way: $M_i = Z^{t_i}$. Using this method provides us with a wider range of size structures. As allometric scaling is an important determinant of biomass dynamics and food web stability (Brose et al. 2006b; Brose 2008), we believe that it is important to investigate its effect on functioning.

For each of these webs, we simulated biomass dynamics using the BioEnergeticFoodWeb package (v. 1.1.2; Delmas et al. 2020), a Julia (v. 1.3.1; Bezanson et al. 2017) implementation of the bioenergetic model as described above in the section Biomass dynamics. Biomass dynamics for each food web were simulated for 3000 time steps (see fig. 4.1, bottom left panel), as systems usually reach the dynamic equilibrium before 1000 time steps. Species extinctions were triggered when species biomass reach 10^{-6}. These extinctions caused a new structure to emerge as all links from and to these species disappear. This emerging structure (see fig. 4.1 right panel) is the one that is later used for the analyses. Codes and data used for these analyses are available at **https://osf.io/yuezq/?view_only=2378095a26d9414489fbcd4a72753a27**.

For every food web that reached equilibrium with three compartments – food webs without secondary consumers were discarded – we estimated its functioning, structure and shape. Functioning here refers to the quantification of the fluxes and stocks within the food webs. Biomass fluxes (represented by arrows in fig. 4.1, right panel) in food webs is the basic process underpinning ecosystem functioning, and reflects many of the functioning typically studied in BEF analyses (Barnes et al. 2018). We thus extracted the biomass values at each time step for all species and calculated fluxes (which correspond here to species intakes, that is $\sum_{\mathrm{k\,=\,resources}} x_i y_i B_i F_{\mathrm{ik}}$ for consumers and $r_i G_i(N) B_i$ for producers) and stocks (total biomass) at the species level using the equations of the model for corresponding process (see the corresponding sections in the sup. mat.). Both the fluxes and stocks were averaged over the second half of the iteration to compensate for potential oscillations. These quantities were later aggregated at the compartment level (plants, primary and secondary consumers) to generate results at the food chain scale. As precision we define omnivores as species that can feed on both animals and producers.

To compare the biomass to intake relationships of communities with and without consumption, we also simulated the biomass dynamics of communities with producers only. As we needed to see a variation in intake, we simulated communities with varying richness (1 to 20) and supply rate (1 to 10). As intake is always close to its maximum value in the absence of consumption, we used a linear regression to extrapolate for a wider range of intake. Without consumption, the relationship between intake and stored biomass should indeed be linear (metabolic losses scale linearly with species biomass).

Structure refers to the organization of trophic interactions between species within the food webs. Once extinct species and the interactions to and from them were discarded, we measured the food web connectance, height (Dunne 2006) and motif profile (Milo 2002). Motifs are the different N-species sub-webs that can exist within a network (here $N = 3$). They are the simplest building blocks of networks. We focused here on 4 motifs that represent fundamental and widely studied trophic modules (omnivory or intraguild predation $A \rightarrow B \rightarrow C \leftarrow A$, food chains $A \rightarrow B \rightarrow C$, apparent $A \leftarrow B \rightarrow C$ and exploitative $A \rightarrow B \leftarrow C$ competition, note that in this paper arrows go from consumer to resource) and have been linked to food web dynamics (Stouffer et al. 2007; Borrelli 2015). We used the Julia package EcologicalNetworks.jl (v0.3.0; Poisot et al. 2020) and the python3 package pymfinder (Mora et al. 2018a) to analyze food web structure.

Food web shape is defined here as what we usually call *trophic structure* in the literature (we decided to use another term to avoid confusion with food webs' network structure). Food web shape describes the distribution of biomass along the three main food chain compartments: plants, primary and secondary consumers. Food webs can have a pyramid or cascade shape, meaning that biomass can be either distributed alternatively or not along the food chain and can be bottom, middle (except for pyramids) or top-heavy (BH, MH or TH), which described the position of the compartment with the highest biomass. In other words, if we order a community compartments (P for producers, H for herbivores and C for secondary consumers) according to their total biomass, if the result is P-H-C, the community has a BH pyramidal shape, P-C-H gives a BH cascade shape, H-C-P and H-P-C both represent MH cascade shape, C-H-P is a TH pyramidal shape (also called inverted pyramid of biomass) and C-P-H is a TH cascade-shaped community.

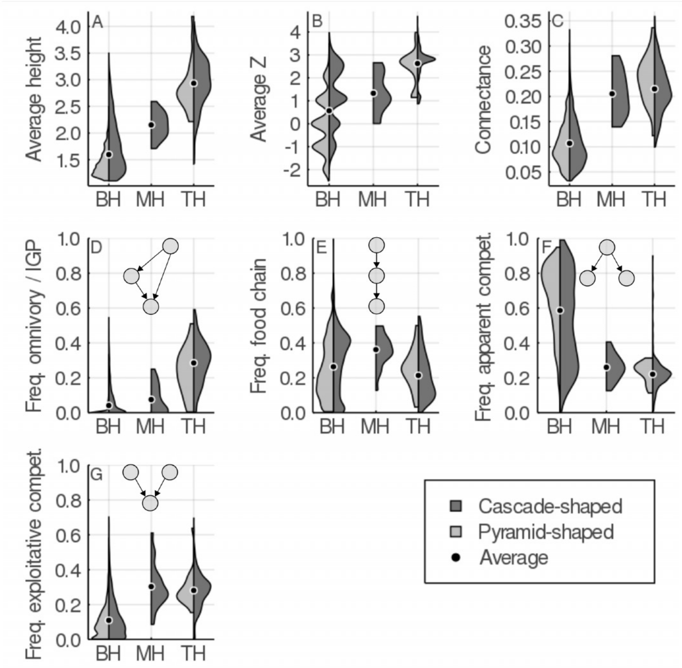


Figure 4.2 Distribution of some food web structural properties of interest. Here are represented the average food web height (maximum trophic level, A), consumer-resource body-size ratio (log10 scale, B), connectance (C), as well as the average frequency of 4 typical motifs in the food webs. These motifs correspond to typical trophic modules: omnivory (or intra-guild predation, D), linear food chain (E), apparent competition (F) and exploitative competition (G). Motifs are represented on top of these panels.

4.3 Results

A total of 4589 food webs persisted with all three compartments (plants, primary and secondary consumers). Among these, a vast majority (91.8 %) are bottom heavy (BH), 7.7 % are top heavy (TH) and only 0.5 % are middle heavy (MH). While there are almost as many bottom-heavy cascade-shaped and pyramid-shaped food webs (50.2 % and 49.8 % respectively), top-heavy food webs are predominantly cascade-shaped (94.6 %). The low proportion of TH pyramid-shaped food webs and MH cascade-shaped food webs make the interpretation of these particular results more difficult. We thus focused our interpretation on either only BH food webs and TH cascade-shaped food webs or qualitative comparisons.

The emergence and persistence of the different shapes seem to be related to feedback between food web functioning and structure. While we were not able to see a sizeable difference

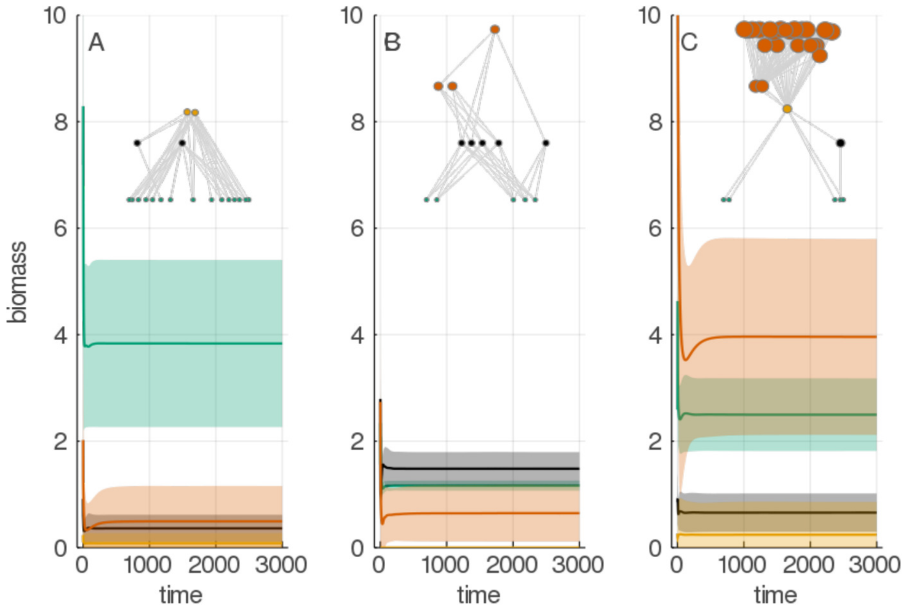


Figure 4.3 Typical food web structure and associated averaged biomass dynamics. Here are represented the average biomass dynamic for the three main compartments, for all bottom-heavy (A), middle-heavy (B) and top-heavy (C) food webs. For each compartment (plants in green, primary consumers in black and secondary consumers in light or dark orange, respectively for omnivores and carnivores), the total compartment biomass is averaged at each time step (solid line) and are represented with standard deviation (ribbon). A typical food web is plotted above the dynamics, following the same colour code. Nodes sizes represent the body mass of the different species (log10 scaled).

in structure between cascade-shaped and pyramid-shaped food webs, we do see structural differences between BH, MH and TH food webs (see fig. 4.2). To better visualize how the different descriptors of structure used in fig. 4.2 translate in terms of food-web global structure, we represented a typical (median values for connectance and height) food webs for each case (fig. 4.3), with the average (solid line) and standard deviation (ribbon) for the biomass dynamics of producers (green), herbivores (black), omnivores (light orange) and carnivores (dark orange). Food webs appear in our analysis to be BH by default, yet TH food webs can still persist but they are relatively rare (7.7 %). These TH food webs exhibit greater vertical diversity (i.e., a greater number of trophic levels; see fig. 4.2 A) allowing them to maintain a higher mean consumer-resource body-mass ratio (see node sizes in the typical food webs, fig. 4.3). This higher ratio is associated with greater stability (Brose et al. 2006b) and large body mass are associated with lower metabolic losses (see model description, appendix 1, section 1 in supplementary material). They are also more complex (higher connectance, see fig. 4.2 C) and display particular types of interactions. In fact, looking at the motifs profile of food webs, it appears that TH food webs have more omnivory/IGP and exploitative competition motifs (fig. 4.2 D and G), while BH food webs have on average more apparent competition motifs (fig. 4.2 D) which seems to be consistent with TH food webs displaying a more complex and functionally diverse secondary consumer compartment. The higher proportion of omnivory is probably related to higher intra-guild predation, causing biomass to potentially take longer paths, and thus have a longer residence time in the system.

Ecological communities in fact appear to be distributed on a multivariate structural gradient according to their top heaviness. On one side of this gradient, we have a very large majority (91.8 %) of bottom heavy communities, presenting a relatively short trophic chain and a fairly low complexity, in the sense that interactions seem to be only slightly entangled (they display a relatively weaker connectivity and less omnivore/intraguild predation motifs, see fig. 4.2 and 4.3). These communities have a high producer species richness at their base, but a low consumer richness (fig. 4.6), thus displaying consumers feeding low in the food chain and often generalists (which is translated by a high proportion of apparent competition motifs as shown in fig. 4.2). In other words, these communities are more horizontally than vertically diverse. Moving along this gradient, we see higher and more complex communities at the other end (connectivity is larger and they have a higher proportion of omnivore/intraguild predation motifs, see fig. 4.2 and 4.3). Conversely, these communities appear to be richer vertically than horizontally. In the middle, in an intermediate situation, there are very few middle-heavy communities. It is important to note however that the range of structural variation produced may be dependent on the food web model used (here the allometric diet breadth model).

Our results indicate that food webs, comprising both competition and consumption, are in general – as expected based on consumption losses– less efficient at storing the captured biomass than purely competitive communities (4.4). The dashed line in each panel of figure fig. 4.4 represents the theoretical biomass to intake regime of community composed of producers only, with no trophic interaction to mediate interspecific competition for the shared nutrients. Intake here represents the food webs total intake, which is equivalent in our model to primary production. We expect that given energetic constraints (metabolism and imperfect assimilation), communities achieve higher biomass, for the same intake, when there are no trophic interactions involved (*e.g.* a grassland with no consumers). The majority of the food webs meets this expectation, displaying a regime below this reference line. Yet, surprisingly, the producers-only baseline regime can be overshot in some cases (approx. 6.4 % of all food webs). This can happen when food webs total intake is above a certain threshold, the value of this intake threshold being dependent on the shape of the food webs. BH food webs (fig. 4.4, D and E) or MH (fig. 4.4, C) have on average a lower biomass to intake regime than TH food webs (fig. 4.4, A and B), which represent a lower ability to store the captured biomass. For example, for a total intake of 0.75, the theoretical relationship for a grassland gives a biomass of approx. 5.5 (fig. 4.4), BH food webs have a biomass largely below this value (< 2.5, fig. 4.4,

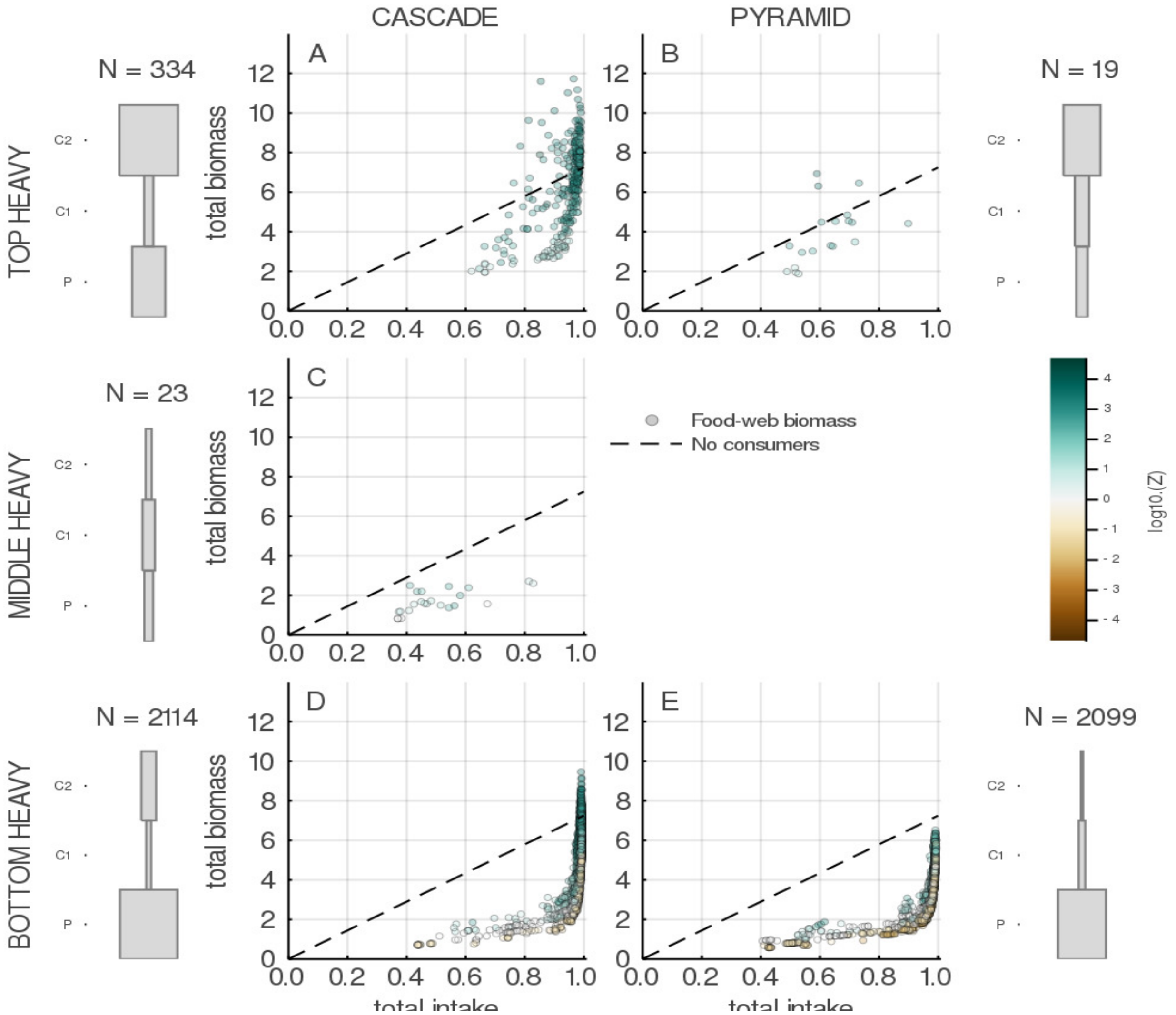


Figure 4.4 Bottom-heavy food webs have a lower biomass turnover on average but can exist at lower intake values and when consumers are on average smaller than their resources (log10(Z) < 0). This figure represents the relationship between food-web total intake and total biomass, or biomass turnover in the food webs (each dots represent one food web) for different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E). Dots are coloured according to the decimal logarithm of the average consumer-resource body-size ratio in the food web. The average shape is represented on the left of each plot for cascades and on the right for pyramids along with N, the amount of food webs in each panel. The grey boxes represent the mean biomass of the three compartments (Plants P, Herbivores C1 and secondary consumers C2).

D and E) but TH food webs have a biomass between 2.5 and 7 (fig. 4.4 A and B), higher than BH and in some case than the theoretical baseline. This does not seem to depend on food webs being pyramid- or cascade-shaped, but only on their top heaviness, although BH cascade-shaped food webs seem not to be able to overshoot the baseline even at maximum intake, unlike their cascade-shaped counterpart. Storage efficiency is also strongly correlated to food webs mean body-size consumer-resource ratio (Z), at the same intake value, higher Z is correlated to higher biomass.

Despite the differences mentioned above, food webs appear to all have qualitatively similar diversity-functioning relationships independently of their shape (fig. 4.6 and fig. 4.5). Total biomass increases with both animal and plant richness with similar rates for all shapes (fig. 4.6), although unfortunately there is not enough variation in food webs displaying TH pyramid or MH shapes to analyze their BEF relationship. Looking at the flows within food webs, we see a similar result, with qualitatively analogous relationship for the different shapes, although it appears that TH pyramid-shaped and MH food webs display a lower level of intake (fig. 4.5). While we reach maximum productivity even for low richness for the BH food webs (fig. 4.5, bottom row), producers appear more strongly controlled in the TH food webs (fig. 4.5, top row) – especially cascade-shaped (fig. 4.5, left column) – and the MH cascades in which herbivores are less regulated (fig. 4.5, C), resulting in low productivity. Consumption, on the other hand is higher, whatever the level of animal richness in the TH food webs (fig. 4.5, top row). This higher consumption is driven mainly by higher secondary consumption, in particular higher intra-guild consumption. In TH and BH cascade-shaped food webs, we see that productivity and secondary consumption both increase with richness while primary consumption decreases (fig. 4.5, A and D). The fact, however, that all richness-functioning relationships are qualitatively similar seems to confirm the existence of a diversity effect, albeit more or less strong depending on shape, in food webs. The qualitative differences are caused by the same synergy of structural (motif distribution) and energetic constraints (consumption and metabolic losses) that give rise to

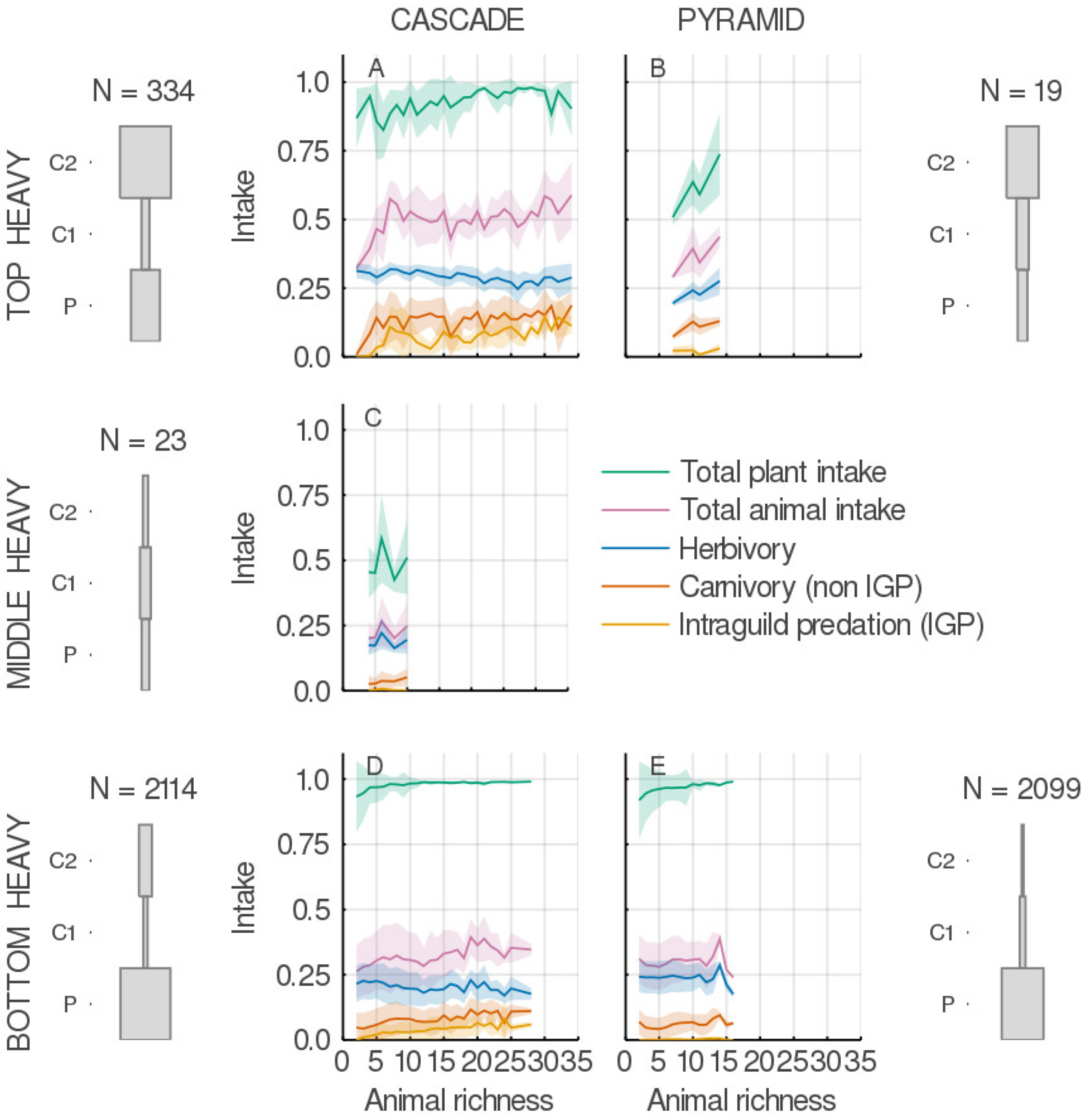


Figure 4.5 Animal richness - flux relationship in food webs with different shapes. This figures shows the effect of total animal richness on food webs total intake for the different compartments (colour coded, see legend) and the different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E). The solid line represents the average response and the shaded area represent the standard deviation around the mean. The average shape is represented on the left of each plot for cascades and on the right for pyramids along with N, the amount of food webs in each panel. The grey boxes represent the mean biomass of the three compartments (Plants P, Herbivores C1 and secondary consumers C2).

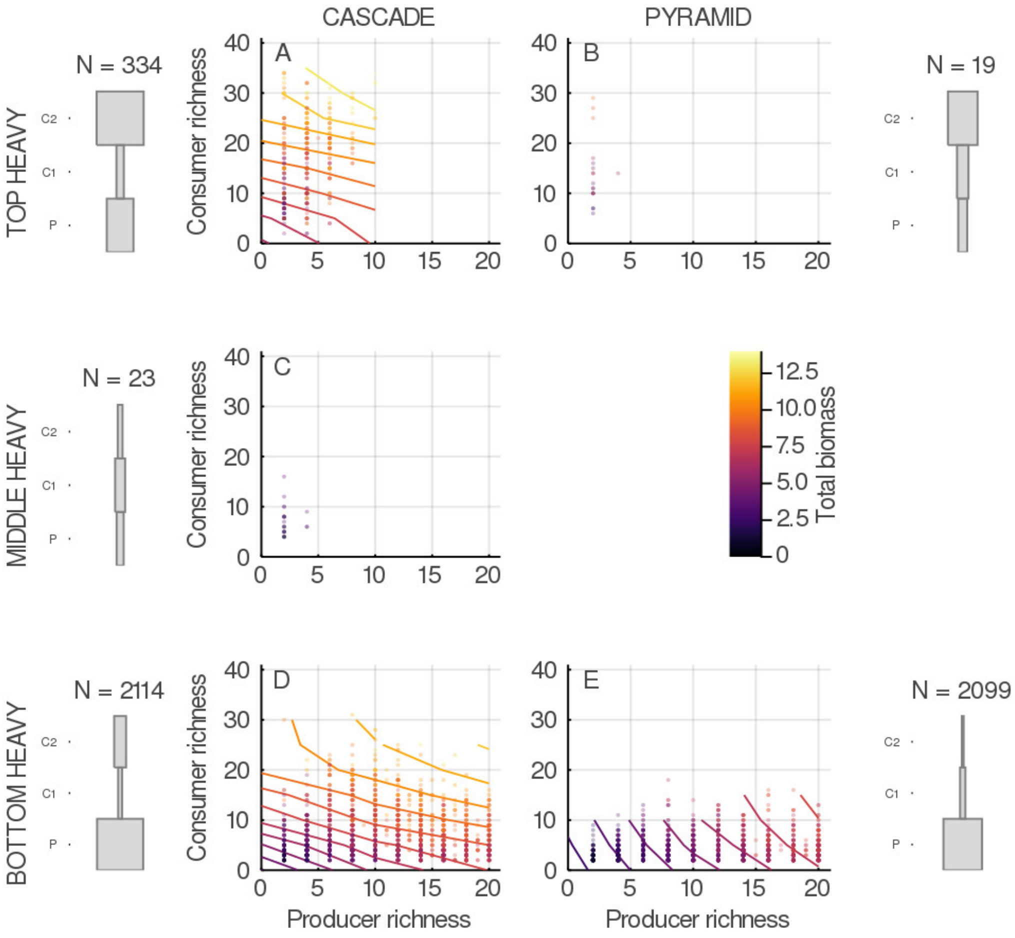


Figure 4.6 Diversity - total biomass relationships in food webs with different shapes. This figures shows the effect of producers and consumers richness on food webs total biomass for food webs of different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E).

either top- or bottom-heavy food webs.

4.4 Discussion

We were able to reproduce predictions typical of different domains of ecology, all of which aim at understanding and predicting ecosystem functioning, but based on different concepts and approaches. On the one hand, the biodiversity-ecosystem functioning (BEF) theory mainly focuses on quantifying the effect of species richness on ecosystem functioning using concepts rooted in competition and predicts a positive and asymptotic BEF relationship (Tilman et al. 1996, 2014; Loreau & Hector 2001). On the other hand, the analysis of biomass transfer in communities represented by trophic chains predicts that communities should be bottom heavy in the absence of biomass or nutrient subsidies (Leroux & Loreau 2008), pyramid-shaped if we adopt a static perspective based on the balance of energy transfers or possibly cascade-shaped if we focus on the dynamics of biomass transfers through trophic interactions (Barbier & Loreau 2019). The methodological framework we used, based on the coupling of the representation of communities through their underlying food webs, and the use of a bioenergetic model to simulate the dynamics of biomass transfers in these trophic networks (Yodzis & Innes 1992; Williams et al. 2007) allows us to integrate concepts deriving from both competition and consumption and thus reconcile the predictions emerging from these concepts.The use of these tools is ultimately what allows us to shed new light on the possible link between these different predictions, and thus on the concepts that frame them.

4.4.1 A link between food webs complexity and top heaviness

When we look at natural ecosystems, we realize that as in our results, they are dominated in most cases by the biomass of heterotrophs (Bar-On et al. 2018). This observation has been at the origin of the bottom-up VS. top-down debate (Wilkinson & Sherratt 2016) as well as much of the work around food chains. In the context of the bioenergetic model, as in nature, energy constraints are such that it is in fact rare to be able to maintain a dominant secondary consumer compartment (Lindeman 1942; McCauley et al. 2018). In addition, the greater risk of extinction faced by predators, especially large top predators (Cardillo 2003; Binzer et al. 2011), add an additional constraint by threatening the persistence of this type of community. This explains why we only find top-heavy food webs at high primary production values (see fig. 4.4). For this to happen in the absence of external factors such as nutrient subsidies (Leroux & Loreau 2008), several conditions must be met, that leads to a particularly efficient system in terms of energy transfer (McCauley et al. 2018). This efficiency, translated in our study by a higher capacity to store the biomass produced (see fig. 4.4), seems to be linked to a particular – more complex – organization of the interactions, and in turn food web structure, as well as to the allometric scaling of biological rates (fig. 4.2).

4.4.2 Similar BEF relationships in spite of different efficiencies at storing biomass

This link between food web structure and biomass turnover is not surprising if we look at recent results on the analysis of biomass dynamics and the resulting functioning in food webs. The use of a very similar methodological framework revealed a correlation between food webs species richness, height and functioning (Wang & Brose 2017), on the one hand, and between species richness, proportion of intraguild predation and functioning, on the other hand (Wang et al. 2019). The fact that we find these two factors (height and proportion of IGP) correlated with communities having higher productivity, biomass (and a lower turnover) seems therefore quite consistent. What is more surprising is that, while the food web structure does have an effect on the distribution of biomass within the different compartments and on the efficiency in storing the biomass produced, this impact has little effect on the diversity-functioning relationship (see fig. 4.5 and 4.6). While we have different vertical vs. horizontal diversity balances — and therefore an equally different competition vs. consumption balance — which should theoretically lead to difference in the BEF relationship (Thébault & Loreau 2006; Duffy et al. 2007) in all cases for which we had enough data to draw conclusions, we have qualitatively very similar (almost identical) diversity-functioning relationships. This is valid whether we look at flows (fig. 4.5) or total biomass (fig. 4.6). In the light of the recent results cited above, that focused on the analysis of the diversity-functioning relationship in food webs, this can be explained by a complex interplay between structure, energy efficiency of interactions, biomass distribution, and functioning. The observed effect of intraguild predation in (Wang et al. 2019) or vertical diversity in (Wang & Brose 2017) would only exist in certain ranges of variation in species richness, which can only persist if the community presents a particularly efficient functioning regime, which leads it to be able to store a large biomass in its apical compartment, i.e., in top-heavy form.

4.4.3 Cascade- and pyramid-shaped food webs are only as different as their top heaviness

It is important to note, however, that although our approach yields communities with different shapes (cascade- and pyramid-shaped), communities' shape does not appear to be related to particular food web structures or to a particular biomass turnover (fig. 4.4). For top-heavy communities, we are potentially limited by the amount of data (only 20 food webs over the total 4589 display an inverted pyramidal shape). The energy constraints are indeed such to maintain a high biomass of carnivores while the biomass of producers is low that it is our understanding that very few communities in the context of our model have been able to persist under these conditions. For bottom-heavy communities, however, we have almost as many pyramid-shaped as we have cascade-shaped communities, and so we do not have this limitation. And there seems to be very little difference between the two, apart from the inability of the bottom-heavy pyramids to overshoot the functioning regime of a purely competitive community. We think this is related to the low relative biomass of carnivores. Indeed, in the cascade-shaped counterpart of the bottom-heavy communities, we note that at high intakes, this baseline is slightly overshot, and that high intakes are generally correlated with high animal diversity. This is what leads us to say that, in the context of our analysis, top heaviness is an important factor in separating communities according to their biomass turnover regime

4.4.4 Perspectives

Other factors limit the scope of our results. In our analysis, we took a non-adaptive view of trophic interactions. Faced with the extinction of some or all of its resources, a consumer in our model cannot adapt by switching its diet, which would result in a rewiring of interactions (Petchey et al. 2008a; Staniczenko et al. 2010; Gilljam et al. 2015). To disentangle the interplay between rewiring (notably through influence on secondary extinction dynamics) according to different rewiring mechanisms and biomass dynamics seems to us to be a necessary first step for the subsequent inclusion of rewiring in this kind of synthesis. It is possible that by allowing consumers to adapt their diet to the biomass variations of their resource or competitor, we see the biomass dynamics change (Kondoh 2003). This in turn could make it easier to maintain structures that would otherwise not be able to persist given energetic constrains, or to maintain a greater range of diversity for certain structures. This could change, if not qualitatively, at least quantitatively our conclusions. It should also be noted that we took a relatively global approach, and chose not to test the effect that ecosystem type might have on our results. Changing the type of ecosystem, and thus the proportion of vertebrates, ectotherm or endotherm vertebrates (which have different biological rates), could also change the results.

Species face increasing extinction risk, threatening the persistence of ecological processes and functioning, but even in systems where species richness is not affected, the structure of the food web that connects them can be altered by environmental changes (Albouy et al. 2014; Kortsch et al. 2015). Ecological network analyses show us that communities are more than the sum of their parts. To maintain ecosystem stability, functioning and the resulting services to human societies, we need to protect the structure of diversity (McCann 2007b;

Tylianakis et al. 2010). Preserving ecological network structure requires that we identify, like we did here, the attributes of network structure that are important ecosystem processes, how species contribute to different attributes, how different attributes interacts and how ecosystem processes feedback on structure. This would ease the choice of conservation targets and make conservation more efficient.

We have emphasized the role of food web structure and its importance to understand ecosystem processes. However, accurately sampling ecological networks such as food webs is not an easy task. When sampling food webs, interactions are established using various methods that reflect different ecological realities (Delmas et al. 2019a). The ensuing difficulty to evaluate food-web data (Jordano 2016) challenges our understanding of the effect of realistic variations in structure, and in turn our ability to make accurate predictions of functioning based on sampled communities. More work in understanding the mechanisms that underlie the probability of an interaction, to build mechanistic food-web models that produce realistic food webs, and more food-web sampling are still needed. However, we show here that precise information may not necessarily be needed. In fact, in the context of our work, species richness of trophic compartments and the animal to producer ratio can be used to estimate the domain of variation of chain length, motifs distribution, and consumer-resource body-mass ratio, which makes estimating the functioning regime of the community possible.

In conclusion, we show here that food web structure is important in understanding ecosystem functioning, but is also the product of feedbacks between species richness and community functioning. If structure does not appear to be influencing qualitatively the diversity-functioning relationship, it still seems important to other aspects of functioning such as the distribution of biomass along the food chain. This in turn could result in different consequences when facing perturbations, as extinction risk increases with trophic rank. Of course, before understanding the real-world implication, more work is needed. Our analysis lays potentially interesting links, the validity and the generality of the relationships between food web structure, top heaviness and functioning regime should be further tested, and the exact mechanisms underlying the relationships identified.

4.5 Supplementary information

4.5.1 The bioenergetic food-web model (BEFWm)

Biomass dynamics in the BEFW model The bioenergetic food web model (Yodzis & Innes 1992; Williams et al. 2007) driving equation is described below (4.2). The first term describes how producers, at the most basal level of the food web, are responsible for biomass growth (thus making $r_i G_i(N) B_i = 0$ for non-producer species). All producers use the same nutrients (N) to produce biomass, sustaining the system. This is described in greater details in the section *Growth through nutrient intake*. Biomass is then transferred through each trophic interaction (second term and third terms of 4.2) through a multi-species functional response (see section *The multi-species functional response*). Finally, biomass is loss through metabolism (fourth term of 4.2).

$$B_i' = r_i G_i(N) B_i - \sum_{\text{j = consumers}} \frac{x_j y_j B_j F_{\text{ji}}}{e_{\text{ji}}} + \sum_{\text{k = resources}} x_i y_i B_i F_{\text{ik}} - x_i B_i \tag{4.2}$$

In 4.2 and the paragraphs below, i represent the focus species, j represent its consumers, k its resources and l the nutrients. The state variable B_i is the biomass of population i. The biomass dependant growth rate of producers is described by the first term of the equation: $r_i G_i(N) B_i$, where r_i is the species intrinsic growth rate and $G_i(N)$ is its net growth rate and depends on nutrients (N) concentration (described below in the paragraph Growth through nutrient intake). The second and third terms of the equation are the biomass transfers (respectively loss and gain) through trophic interactions between population i, its consumers j and resources k. It depends on the consumer (j or i) mass-specific metabolic rate (x), its maximum consumption rate relative to its metabolic rate (y), a multi-resource functional response (F, described in more details below in the paragraph *Consumption: the multi-species functional response*) and i's assimilation efficiency when consuming population j (e_{ij}). Finally, all species lose biomass through metabolism, this is described by the last term of 4.2. The values chosen for all parameters are given in table S4.1.

Table S4.1 Values used for the parameters of the bioenergetic model. The metabolic rate x is allometrically scaled and as such is different for each species. Parameter values from Brose et al., 2006 and Brose, 2008.

Parameter	Symbol	Value
Intrinsic growth rate	r_i	1
Metabolic rate	x_i	See appendix
Maximum assimilation rate	y_i	8 for invertebrates, 4 for vertebrates
Assimilation efficiency	$e_j i$	0.85 for carnivory links, 0.45 otherwise
Plants half-saturation densities	K_{li}	$\mathcal{U} \sim [0.15, 0.20]$
Turnover rate	D	0.25
Supply	S_l	4 for each nutrient
Nutrient content in plant biomass	c_l	$c_1 = 1$ and $c_2 0.5$
Preference	ω_{ji}	$1/n$ where n is the number of resources
Consumers half-saturation densities	B_0	0.5
Hill exponent	h	2
Predator interference	c	0

Growth through nutrient intake The nutrient intake model (Tilman et al. 1996; Brose et al. 2005a) describes the relationship between nutrient concentration and producer biomass, and is formalized by the following equation:

$$G_i(N) = MIN(\frac{N_1}{K_{1\mathrm{i}} + N_1}, \frac{N_2}{K_{2\mathrm{i}} + N_2}) \tag{4.3}$$

In 4.3 N_1 and N_2 are the respective concentrations in the environment of the two nutrients shared by all plant species. Competition between plants emerge from this model through the difference in the plants half-saturation density (K_{li}) for the two nutrients. The concentration of the two nutrients is determined by the following equation:

$$N_l' = D(S_l - N_l) - \sum_{\mathrm{i\,=\,1}}^{n}(c_{\mathrm{li}} r_i G_i(N) B_i) \tag{4.4}$$

where D is the turnover rate relative to the time scale of the system (determined by the intrinsic growth rate), S_l is the supply concentration and c_{li} is the concentration of nutrient l in species i, which determines which of the two nutrient species need the most. If plants intrinsic growth rate r, metabolic rate x and concentration for each nutrient c_1 and c_2 are equal, then the hierarchy of competition is primarily determined by species half saturation for $K_{1\mathrm{i}}$ (the smaller the stronger competitor i is) if $c_1 > c_2$ and conversely.

The multi-species functional response The second and third terms of 4.2 describe respectively the amount of biomass lost and gained through consuming or being consumed by other species. While $(x_i y_i B_i)/e_{\mathrm{ji}}$ determines the metabolic-dependant efficiency of i at consuming j, F_{ji} expresses the fraction of this efficiency rate that is actually achieved by j when consuming i. This fraction, namely the functional response, is expressed through the following equation:

$$F_{\mathrm{ik}} = \frac{\omega_{\mathrm{ik}} B_k^h}{B_0^h + cB_i B_0^h + \sum_{\mathrm{r\,=\,resources}} \omega_{\mathrm{ir}} B_r^h} \tag{4.5}$$

where ω_{ik} quantify the specialization of i towards k, that is the fraction of i's diet (represented by the maximum consumption rate y_i) targeted to eating k. The parameter h, the Hill exponent, controls how the functional response will saturate in response to an increase in k's biomass (B_k). Hill coefficient is bound between 1 (Holling type II functional response; Holling 1959) and 2 (Holling type III functional response, Holling 1959; Real 1977), but can take any value in between, making the saturation curve more or less sigmoid. Predator interference can also be implemented in this functional response by making $c > 0$, which expresses the density-dependant control of predators on themselves (DeAngelis et al. 1975). Finally, B_0 represent the half-saturation density.

4.5.2 The allometric diet-breadth model (ADBm)

To predict interactions between species, the ADBm (Petchey et al. 2008a) works in two steps. First it calculates the profitability (P_{ij}, or rate of energy intake) for each pair of species in the community. Then, it selects the links that maximize it. Profitability is expressed as:

$$P_{\mathrm{ij}} = \frac{\sum_{\mathrm{i\,=\,1}} \lambda_{\mathrm{ij}} E_i}{1 + \sum_{\mathrm{i\,=\,1}} \lambda_{\mathrm{ij}} H_{\mathrm{ij}}} \tag{4.6}$$

where, E_i is the net energy gained by j when consuming i and scales linearly with i's body size (M_i): $E_i = eM_i$. Profitability also depends on the encounter rates λ_{ij} ($\lambda_{\mathrm{ij}} = N_i * A_{ij}$) which depends on the density of the resource species ($N_i = nM_i$) and the attack rate ($A_{ij} = aM_i^{a_i} M_j^{a_j}$). Finally, profitability is also influenced by the handling time H_{ij}. We chose to implement the "ratio" method for estimating handling time as it is supposed to yield more accurate results. In this formulation, handling time is estimated differently depending on the body-size ratio between a consumer and its potential prey. If the size different is too big (bigger than a chosen threshold b) then we assume that i is not able to consume j. This is expressed by having $H_{ij} = h/(b - (M_i/M_j))$ if $M_i/M_j > b$ and $H_{ij} = \inf$ otherwise. Parameters values are presented below in the S4.2.

Table S4.2 Values used for the parameters of the allometric diet breadth model. For more details and references for the parameters values used, see Petchey et al., 2008.

Parameter	Symbol	Value
Allometric constant for attack rate	a	0.0189
Consumers allometric coefficient for attack rate	a_i	-0.491
Resources allometric coefficient for attack rate	a_j	-0.465
Allometric constant for handling time	h	1
Threshold for handling time	b	0.401

4.5.3 The Benguela pelagic food web

We used body mass data from species of the Benguela upwelling system, as described in Yodzis (1998) and Brose et al. (2016). From the complete list of interactions, we only kept herbivorous and predacious links and discarded bacterivorous links. The heterotrophic producers were identified as the resource of herbivorous interactions. We sampled body masses from species mean body mass data, and recorded the metabolic type associated with it. The following table provides a list of all species with their body mass and metabolic type.

Table S4.3 Herbivorous and predacious interactions in the Benguela pelagic food web associated with species common names, body masses and metabolic classes.

Interaction type	Consumer species	Consumer metab	Consumer mass	Resource species	Resource metab	Resource mass
herbivorous	Bacteria	heterotrophic bacteria	1.0e-8	Phytoplankton	photo-autotroph	0.0001
predacious	Benthic carnivores	invertebrate	10	Benthic filter feeders	invertebrate	10
herbivorous	Microzooplankton	invertebrate	0.0001	Phytoplankton	photo-autotroph	0.0001
predacious	Microzooplankton	invertebrate	0.0001	Microzooplankton	invertebrate	0.0001
herbivorous	Mesozooplankton	invertebrate	0.01	Phytoplankton	photo-autotroph	0.0001
predacious	Mesozooplankton	invertebrate	0.01	Microzooplankton	invertebrate	0.0001
herbivorous	Macrozooplankton	invertebrate	1	Phytoplankton	photo-autotroph	0.0001
predacious	Macrozooplankton	invertebrate	1	Mesozooplankton	invertebrate	0.01
predacious	Macrozooplankton	invertebrate	1	Macrozooplankton	invertebrate	1
herbivorous	Gelatinous zooplankton	invertebrate	100	Phytoplankton	photo-autotroph	0.0001
predacious	Gelatinous zooplankton	invertebrate	100	Microzooplankton	invertebrate	0.0001
predacious	Gelatinous zooplankton	invertebrate	100	Macrozooplankton	invertebrate	1
herbivorous	Anchovy	ectotherm vertebrate	11.5	Phytoplankton	photo-autotroph	0.0001
predacious	Anchovy	ectotherm vertebrate	11.5	Microzooplankton	invertebrate	0.0001
predacious	Anchovy	ectotherm vertebrate	11.5	Macrozooplankton	invertebrate	1
herbivorous	Pilchard	ectotherm vertebrate	280	Phytoplankton	photo-autotroph	0.0001
predacious	Pilchard	ectotherm vertebrate	280	Macrozooplankton	invertebrate	1
predacious	Round herring	ectotherm vertebrate	215.2	Macrozooplankton	invertebrate	1
predacious	Lightfish	ectotherm vertebrate	4.8	Macrozooplankton	invertebrate	1
predacious	Lanternfish	ectotherm vertebrate	6.9	Macrozooplankton	invertebrate	1
herbivorous	Goby	ectotherm vertebrate	18.6	Phytoplankton	photo-autotroph	0.0001
predacious	Goby	ectotherm vertebrate	18.6	Macrozooplankton	invertebrate	1
predacious	Other pelagics	ectotherm vertebrate	2554.85	Benthic carnvores	invertebrate	10
predacious	Other pelagics	ectotherm vertebrate	2554.85	Macrozooplankton	invertebrate	1
predacious	Other pelagics	ectotherm vertebrate	2554.85	Gelatinous zooplankton	invertebrate	100
predacious	Horse mackerel	ectotherm vertebrate	5104.9	Lanternfish	ectotherm vertebrate	6.9
predacious	Horse mackerel	ectotherm vertebrate	5104.9	Benthic carnivores	invertebrate	10
predacious	Horse mackerel	ectotherm vertebrate	5104.9	Macrozooplankton	invertebrate	1
predacious	Chub mackerel	ectotherm vertebrate	3259.5	Lanternfish	ectotherm vertebrate	6.9
predacious	Chub mackerel	ectotherm vertebrate	3259.5	Benthic carnivores	invertebrate	10
predacious	Chub mackerel	ectotherm vertebrate	3259.5	Macrozooplankton	invertebrate	1
predacious	Chub mackerel	ectotherm vertebrate	3259.5	Round herring	ectotherm vertebrate	215.2
predacious	Other groundfish	ectotherm vertebrate	13127	Round herring	ectotherm vertebrate	215.2
predacious	Other groundfish	ectotherm vertebrate	13127	Lightfish	ectotherm vertebrate	4.8
predacious	Other groundfish	ectotherm vertebrate	13127	Lanternfish	ectotherm vertebrate	6.9
predacious	Other groundfish	ectotherm vertebrate	13127	Goby	ectotherm vertebrate	18.6

predacious	Other groundfish	ectotherm vertebrate	13127	Other pelagics	ectotherm vertebrate	2554.85
predacious	Other groundfish	ectotherm vertebrate	13127	Other groundfish	ectotherm vertebrate	13127
predacious	Other groundfish	ectotherm vertebrate	13127	Hakes	ectotherm vertebrate	22994.5
predacious	Other groundfish	ectotherm vertebrate	13127	Squid	invertebrate	40
predacious	Other groundfish	ectotherm vertebrate	13127	Benthic carnivores	invertebrate	10
predacious	Other groundfish	ectotherm vertebrate	13127	Mesozooplankton	invertebrate	0.01
predacious	Other groundfish	ectotherm vertebrate	13127	Macrozooplankton	invertebrate	1
predacious	Other groundfish	ectotherm vertebrate	13127	Anchovy	ectotherm vertebrate	11.5
predacious	Hakes	ectotherm vertebrate	22994.5	Pilchard	ectotherm vertebrate	280
predacious	Hakes	ectotherm vertebrate	22994.5	Round herring	ectotherm vertebrate	215.2
predacious	Hakes	ectotherm vertebrate	22994.5	Lightfish	ectotherm vertebrate	4.8
predacious	Hakes	ectotherm vertebrate	22994.5	Lanternfish	ectotherm vertebrate	6.9
predacious	Hakes	ectotherm vertebrate	22994.5	Goby	ectotherm vertebrate	18.6
predacious	Hakes	ectotherm vertebrate	22994.5	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Hakes	ectotherm vertebrate	22994.5	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Hakes	ectotherm vertebrate	22994.5	Other groundfish	ectotherm vertebrate	13127
predacious	Hakes	ectotherm vertebrate	22994.5	Hakes	ectotherm vertebrate	22994.5
predacious	Hakes	ectotherm vertebrate	22994.5	Squid	invertebrate	40
predacious	Hakes	ectotherm vertebrate	22994.5	Mesozooplankton	invertebrate	0.01
predacious	Hakes	ectotherm vertebrate	22994.5	Macrozooplankton	invertebrate	1
predacious	Hakes	ectotherm vertebrate	22994.5	Anchovy	ectotherm vertebrate	11.5
predacious	Squid	invertebrate	40	Pilchard	ectotherm vertebrate	280
predacious	Squid	invertebrate	40	Round herring	ectotherm vertebrate	215.2
predacious	Squid	invertebrate	40	Lightfish	ectotherm vertebrate	4.8
predacious	Squid	invertebrate	40	Goby	ectotherm vertebrate	18.6
predacious	Squid	invertebrate	40	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Squid	invertebrate	40	Other groundfish	ectotherm vertebrate	13127
predacious	Squid	invertebrate	40	Hakes	ectotherm vertebrate	22994.5
predacious	Squid	invertebrate	40	Squid	invertebrate	40
predacious	Squid	invertebrate	40	Benthic carnivores	invertebrate	10
predacious	Squid	invertebrate	40	Macrozooplankton	invertebrate	1
predacious	Squid	invertebrate	40	Anchovy	ectotherm vertebrate	11.5
predacious	Tunas	ectotherm vertebrate	909000	Pilchard	ectotherm vertebrate	280
predacious	Tunas	ectotherm vertebrate	909000	Round herring	ectotherm vertebrate	215.2
predacious	Tunas	ectotherm vertebrate	909000	Lightfish	ectotherm vertebrate	4.8
predacious	Tunas	ectotherm vertebrate	909000	Lanternfish	ectotherm vertebrate	6.9
predacious	Tunas	ectotherm vertebrate	909000	Goby	ectotherm vertebrate	18.6
predacious	Tunas	ectotherm vertebrate	909000	Other pelagics	ectotherm vertebrate	2554.85
predacious	Tunas	ectotherm vertebrate	909000	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Tunas	ectotherm vertebrate	909000	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Tunas	ectotherm vertebrate	909000	Hakes	ectotherm vertebrate	22994.5
predacious	Tunas	ectotherm vertebrate	909000	Squid	invertebrate	40
predacious	Tunas	ectotherm vertebrate	909000	Benthic carnivores	invertebrate	10
predacious	Tunas	ectotherm vertebrate	909000	Anchovy	ectotherm vertebrate	11.5
predacious	Snoek	ectotherm vertebrate	13012.1	Pilchard	ectotherm vertebrate	280
predacious	Snoek	ectotherm vertebrate	13012.1	Round herring	ectotherm vertebrate	215.2
predacious	Snoek	ectotherm vertebrate	13012.1	Lightfish	ectotherm vertebrate	4.8
predacious	Snoek	ectotherm vertebrate	13012.1	Lanternfish	ectotherm vertebrate	6.9
predacious	Snoek	ectotherm vertebrate	13012.1	Goby	ectotherm vertebrate	18.6
predacious	Snoek	ectotherm vertebrate	13012.1	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Snoek	ectotherm vertebrate	13012.1	Hakes	ectotherm vertebrate	22994.5
predacious	Snoek	ectotherm vertebrate	13012.1	Squid	invertebrate	40
predacious	Snoek	ectotherm vertebrate	13012.1	Benthic carnivores	invertebrate	10
predacious	Snoek	ectotherm vertebrate	13012.1	Macrozooplankton	invertebrate	1
predacious	Snoek	ectotherm vertebrate	13012.1	Anchovy	ectotherm vertebrate	11.5
predacious	Kob	ectotherm vertebrate	68000	Pilchard	ectotherm vertebrate	280

predacious	Kob	ectotherm vertebrate	68000	Goby	ectotherm vertebrate	18.6
predacious	Kob	ectotherm vertebrate	68000	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Kob	ectotherm vertebrate	68000	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Kob	ectotherm vertebrate	68000	Other groundfish	ectotherm vertebrate	13127
predacious	Kob	ectotherm vertebrate	68000	Hakes	ectotherm vertebrate	22994.5
predacious	Kob	ectotherm vertebrate	68000	Squid	invertebrate	40
predacious	Kob	ectotherm vertebrate	68000	Kob	ectotherm vertebrate	68000
predacious	Kob	ectotherm vertebrate	68000	Benthic carnivores	invertebrate	10
predacious	Kob	ectotherm vertebrate	68000	Macrozooplankton	invertebrate	1
predacious	Kob	ectotherm vertebrate	68000	Anchovy	ectotherm vertebrate	11.5
predacious	Yellowtail	ectotherm vertebrate	82040.3	Pilchard	ectotherm vertebrate	280
predacious	Yellowtail	ectotherm vertebrate	82040.3	Round herring	ectotherm vertebrate	215.2
predacious	Yellowtail	ectotherm vertebrate	82040.3	Goby	ectotherm vertebrate	18.6
predacious	Yellowtail	ectotherm vertebrate	82040.3	Other pelagics	ectotherm vertebrate	2554.85
predacious	Yellowtail	ectotherm vertebrate	82040.3	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Yellowtail	ectotherm vertebrate	82040.3	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Yellowtail	ectotherm vertebrate	82040.3	Other groundfish	ectotherm vertebrate	13127
predacious	Yellowtail	ectotherm vertebrate	82040.3	Squid	invertebrate	40
predacious	Yellowtail	ectotherm vertebrate	82040.3	Macrozooplankton	invertebrate	1
predacious	Yellowtail	ectotherm vertebrate	82040.3	Anchovy	ectotherm vertebrate	11.5
predacious	Geelbek	ectotherm vertebrate	26127.38	Pilchard	ectotherm vertebrate	280
predacious	Geelbek	ectotherm vertebrate	26127.38	Round herring	ectotherm vertebrate	215.2
predacious	Geelbek	ectotherm vertebrate	26127.38	Goby	ectotherm vertebrate	18.6
predacious	Geelbek	ectotherm vertebrate	26127.38	Other pelagics	ectotherm vertebrate	2554.85
predacious	Geelbek	ectotherm vertebrate	26127.38	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Geelbek	ectotherm vertebrate	26127.38	Other groundfish	ectotherm vertebrate	13127
predacious	Geelbek	ectotherm vertebrate	26127.38	Hakes	ectotherm vertebrate	22994.5
predacious	Geelbek	ectotherm vertebrate	26127.38	Squid	invertebrate	40
predacious	Geelbek	ectotherm vertebrate	26127.38	Benthic carnivores	invertebrate	10
predacious	Geelbek	ectotherm vertebrate	26127.38	Anchovy	ectotherm vertebrate	11.5
predacious	Whales and Dolphins	endotherm vertebrate	82000	Pilchard	ectotherm vertebrate	280
predacious	Whales and Dolphins	endotherm vertebrate	82000	Round herring	ectotherm vertebrate	215.2
predacious	Whales and Dolphins	endotherm vertebrate	82000	Lanternfish	ectotherm vertebrate	6.9
predacious	Whales and Dolphins	endotherm vertebrate	82000	Goby	ectotherm vertebrate	18.6
predacious	Whales and Dolphins	endotherm vertebrate	82000	Other pelagics	ectotherm vertebrate	2554.85
predacious	Whales and Dolphins	endotherm vertebrate	82000	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Whales and Dolphins	endotherm vertebrate	82000	Hakes	ectotherm vertebrate	22994.5
predacious	Whales and Dolphins	endotherm vertebrate	82000	Squid	invertebrate	40
predacious	Whales and Dolphins	endotherm vertebrate	82000	Macrozooplankton	invertebrate	1
predacious	Whales and Dolphins	endotherm vertebrate	82000	Anchovy	ectotherm vertebrate	11.5
predacious	Birds	endotherm vertebrate	2287	Pilchard	ectotherm vertebrate	280
predacious	Birds	endotherm vertebrate	2287	Round herring	ectotherm vertebrate	215.2
predacious	Birds	endotherm vertebrate	2287	Lightfish	ectotherm vertebrate	4.8
predacious	Birds	endotherm vertebrate	2287	Lanternfish	ectotherm vertebrate	6.9
predacious	Birds	endotherm vertebrate	2287	Goby	ectotherm vertebrate	18.6
predacious	Birds	endotherm vertebrate	2287	Other pelagics	ectotherm vertebrate	2554.85
predacious	Birds	endotherm vertebrate	2287	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Birds	endotherm vertebrate	2287	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Birds	endotherm vertebrate	2287	Other groundfish	ectotherm vertebrate	13127
predacious	Birds	endotherm vertebrate	2287	Hakes	ectotherm vertebrate	22994.5
predacious	Birds	endotherm vertebrate	2287	Squid	invertebrate	40
predacious	Birds	endotherm vertebrate	2287	Snoek	ectotherm vertebrate	13012.1
predacious	Birds	endotherm vertebrate	2287	Birds	endotherm vertebrate	2287
predacious	Birds	endotherm vertebrate	2287	Seals	endotherm vertebrate	136000
predacious	Birds	endotherm vertebrate	2287	Benthic carnivores	invertebrate	10
predacious	Birds	endotherm vertebrate	2287	Mesozooplankton	invertebrate	0.01

predacious	Birds	endotherm vertebrate	2287	Macrozooplankton	invertebrate	1
predacious	Birds	endotherm vertebrate	2287	Anchovy	ectotherm vertebrate	11.5
predacious	Seals	endotherm vertebrate	136000	Pilchard	ectotherm vertebrate	280
predacious	Seals	endotherm vertebrate	136000	Round herring	ectotherm vertebrate	215.2
predacious	Seals	endotherm vertebrate	136000	Lightfish	ectotherm vertebrate	4.8
predacious	Seals	endotherm vertebrate	136000	Lanternfish	ectotherm vertebrate	6.9
predacious	Seals	endotherm vertebrate	136000	Goby	ectotherm vertebrate	18.6
predacious	Seals	endotherm vertebrate	136000	Other pelagics	ectotherm vertebrate	2554.85
predacious	Seals	endotherm vertebrate	136000	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Seals	endotherm vertebrate	136000	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Seals	endotherm vertebrate	136000	Other groundfish	ectotherm vertebrate	13127
predacious	Seals	endotherm vertebrate	136000	Hakes	ectotherm vertebrate	22994.5
predacious	Seals	endotherm vertebrate	136000	Squid	invertebrate	40
predacious	Seals	endotherm vertebrate	136000	Snoek	ectotherm vertebrate	13012.1
predacious	Seals	endotherm vertebrate	136000	Birds	endotherm vertebrate	2287
predacious	Seals	endotherm vertebrate	136000	Sharks	ectotherm vertebrate	1500
predacious	Seals	endotherm vertebrate	136000	Benthic carnivores	invertebrate	10
predacious	Seals	endotherm vertebrate	136000	Anchovy	ectotherm vertebrate	11.5
predacious	Sharks	ectotherm vertebrate	1500	Pilchard	ectotherm vertebrate	280
predacious	Sharks	ectotherm vertebrate	1500	Round herring	ectotherm vertebrate	215.2
predacious	Sharks	ectotherm vertebrate	1500	Lightfish	ectotherm vertebrate	4.8
predacious	Sharks	ectotherm vertebrate	1500	Goby	ectotherm vertebrate	18.6
predacious	Sharks	ectotherm vertebrate	1500	Other pelagics	ectotherm vertebrate	2554.85
predacious	Sharks	ectotherm vertebrate	1500	Horse mackerel	ectotherm vertebrate	5104.9
predacious	Sharks	ectotherm vertebrate	1500	Chub mackerel	ectotherm vertebrate	3259.5
predacious	Sharks	ectotherm vertebrate	1500	Other groundfish	ectotherm vertebrate	13127
predacious	Sharks	ectotherm vertebrate	1500	Hakes	ectotherm vertebrate	22994.5
predacious	Sharks	ectotherm vertebrate	1500	Squid	invertebrate	40
predacious	Sharks	ectotherm vertebrate	1500	Tunas	ectotherm vertebrate	909000
predacious	Sharks	ectotherm vertebrate	1500	Snoek	ectotherm vertebrate	13012.1
predacious	Sharks	ectotherm vertebrate	1500	Kob	ectotherm vertebrate	68000
predacious	Sharks	ectotherm vertebrate	1500	Yellowtail	ectotherm vertebrate	82040.3
predacious	Sharks	ectotherm vertebrate	1500	Geelbek	ectotherm vertebrate	26127.38
predacious	Sharks	ectotherm vertebrate	1500	Whales and Dolphins	endotherm vertebrate	82000
predacious	Sharks	ectotherm vertebrate	1500	Birds	endotherm vertebrate	2287
predacious	Sharks	ectotherm vertebrate	1500	Seals	endotherm vertebrate	136000
predacious	Sharks	ectotherm vertebrate	1500	Sharks	ectotherm vertebrate	1500
predacious	Sharks	ectotherm vertebrate	1500	Benthic carnivores	invertebrate	10
predacious	Sharks	ectotherm vertebrate	1500	Mesozooplankton	invertebrate	0.01
predacious	Sharks	ectotherm vertebrate	1500	Macrozooplankton	invertebrate	1
predacious	Sharks	ectotherm vertebrate	1500	Anchovy	ectotherm vertebrate	11.5

4.5.4 Breaking down of the diversity-functioning relationship

Figure S4.1 Animal to producer biomass ratio for different levels of diversity. This figures shows the relationship between producers and consumers richness on food webs animal to producer biomass ratio for food webs of different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E).

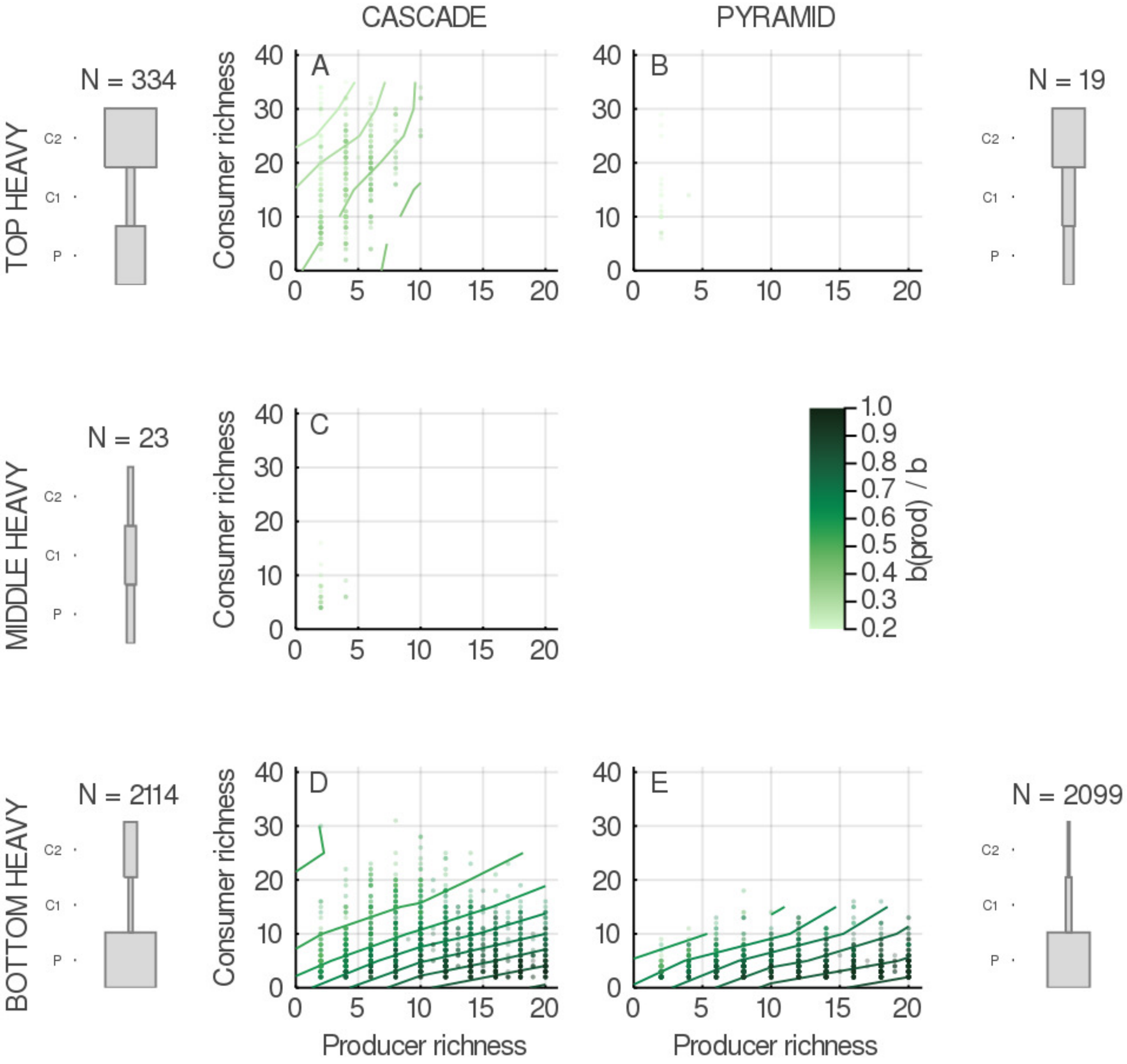


Figure S4.2 Diversity - total primary production relationships in food webs. This figures shows the effect of producers and consumers richness on food webs total primary production for food webs of different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E).

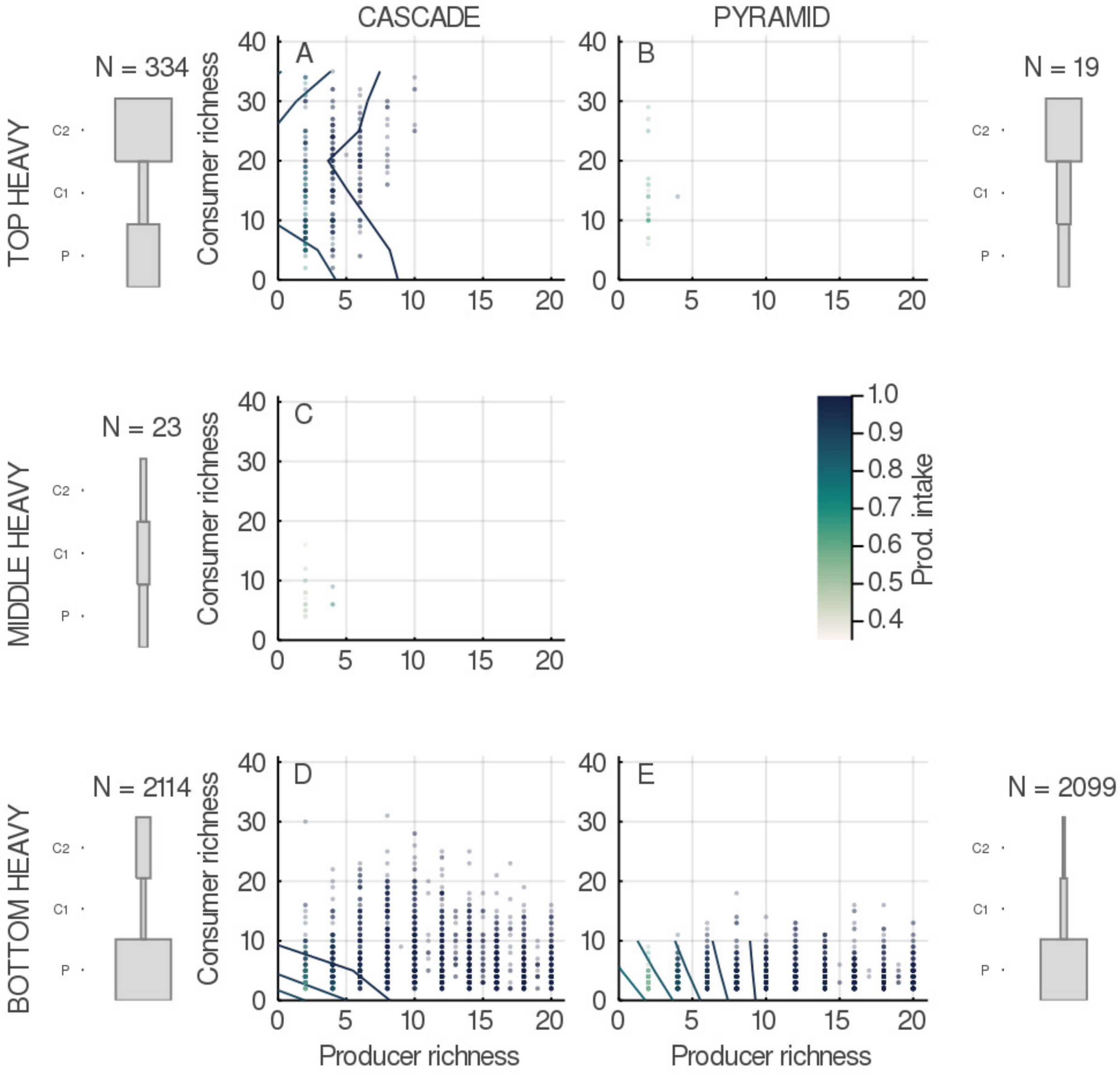


Figure S4.3 Diversity - total herbivory relationships in food webs. This figures shows the effect of producers and consumers richness on food webs total consumption by herbivores for food webs of different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E).

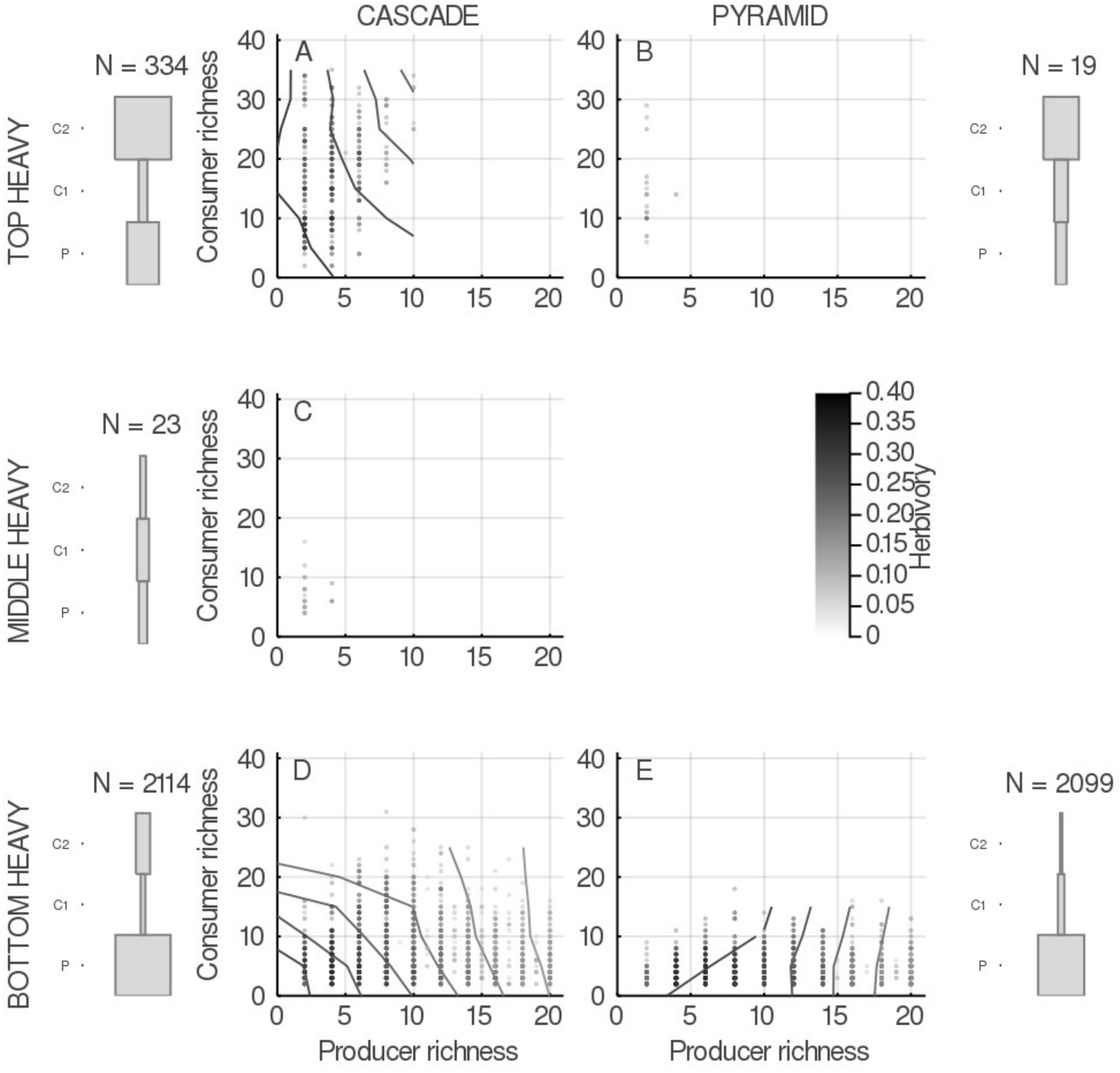
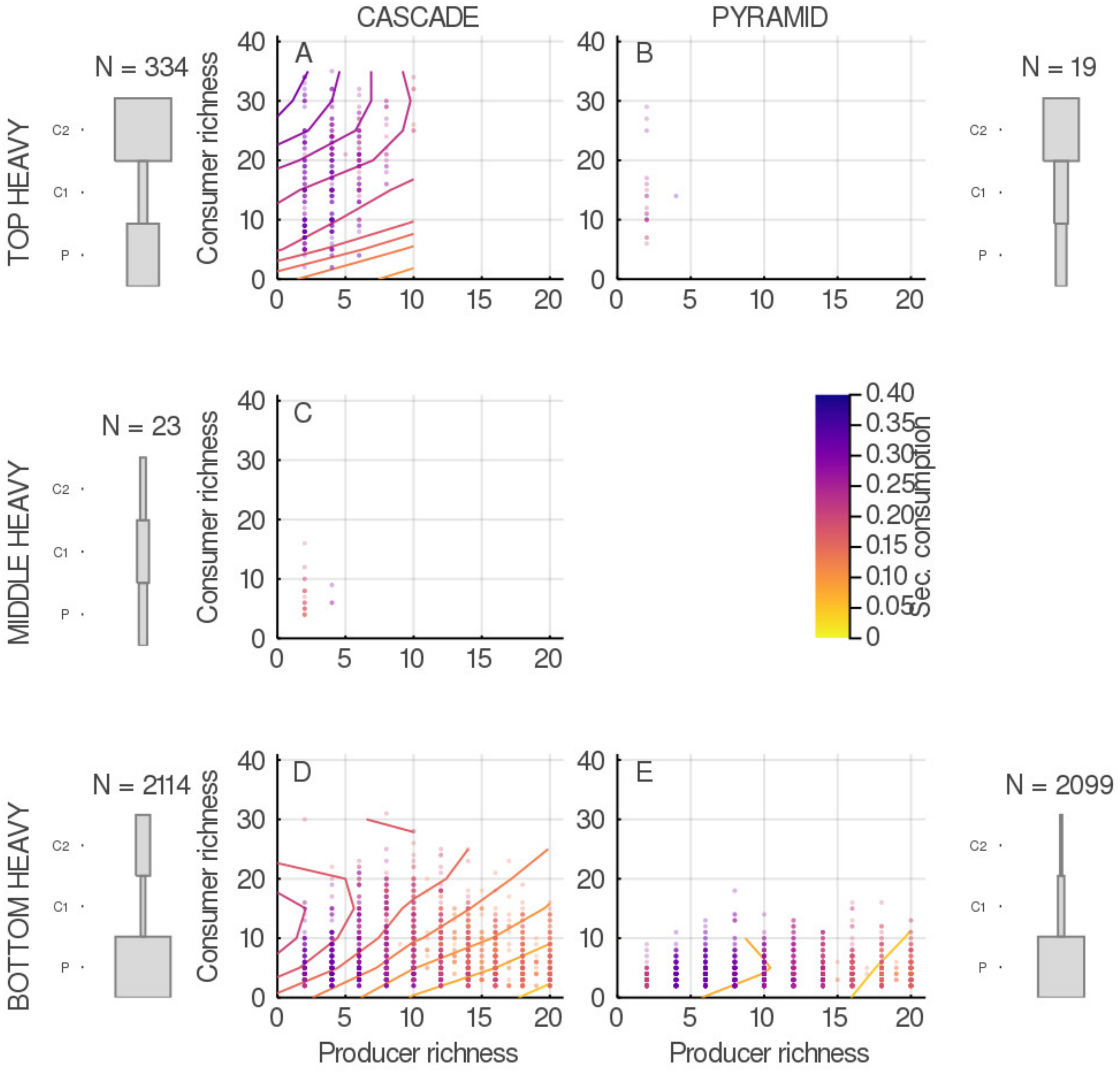


Figure S4.4 Diversity - total secondary consumption relationships in food webs. This figures shows the effect of producers and consumers richness on food webs total secondary consumption for food webs of different shapes, namely top-heavy (top, A and B), medium-heavy (middle row, C) and bottom-heavy (bottom, D and E) cascades (left, A, C and D) and pyramids (right, B and E).



Chapter 5

Conclusion

An alligator, top predator of the swamps, eating a fish near New Orleans, Louisiana.

The main objective of this thesis is to understand **how food-web structure influences the BEF relationships in complex ecological communities**. I have chosen to reach this goal not only by performing a set of experiments and analyses but also by assessing the existing methodological framework traditionally used for this type of issue; and by identifying and implementing in a common and open platform a set of existing tools that, in my opinion, are necessary to advance the field more robustly and rapidly.

I first chose and implemented a model to adequately simulate biomass dynamics in food webs, accounting for traits of fundamental importance for estimating species biological rates (body mass and metabolic class): the bioenergetic food-web model (BEFWm; Yodzis & Innes 1992; Williams et al. 2007). This model is probably the most widely used to investigate food web functioning and the BEF relationships in complex communities (see [table S2.1][List of published papers since 2007 that have used the bioenergetic food-web model.]). We published the BEFWm in a library – `BioEnergeticFoodWeb.jl` – to provide an open platform for further synthesis and comparison, using one of the highest performances, dynamic, and easy-to-use language: `Julia`. We also added a wide set of tests to make sure that the results can be trusted, and assessed its ability to reproduce previous results, a necessary step for synthesis. I describe this model and its use in **chapter 2**, and provide an overview of the new features that were later added in the following discussion. Simulating realistic biomass dynamics in species- and link-rich food webs gives the possibility to estimate various measures of functioning, by quantifying the flows and stocks at different organizational levels (species, trophic levels, trophic compartments, etc.). However to understand how food-web structure influences functioning, we also needed to choose how to measure significant aspects of structure, that quantify the ecological properties most likely to drive functioning.

Realizing the lack of a comprehensive review of the wide set of existing methods for describing ecological networks, we decided to write it. **Chapter 3** is not an exhaustive review of all available methods, but gives an overview of robust and informative tools, as well as the ecological properties and processes they can abstract, and their limitations. In other words, we have tried to outline the "best practices" for the field. This served as a basis for the `EcologicalNetworks.jl` package, by Poisot et al. (2020), for ecological networks analysis. This review also later helped me choose how to measure informative structural attributes, likely to shape biomass dynamics in food webs.

Finally, in **chapter 4**, I built on these methodological steps, and used the `BioEnergeticFoodWebs .jl` package to simulate biomass dynamics in realistic food webs, with varying structures, diversity and body-mass distributions. I used food web analysis to investigate the influence of food web structure on the BEF relationships in complex ecological communities. In this chapter I used concepts from diverging fields of ecology — BEF and food-chain analyses — and show how food web structure helps us understand how their respective predictions fit together and how it helps us understand the BEF relationships in complex ecological communities.

5.1 A relationship between communities top-heaviness, food-web complexity and functioning.

The BEFWm has been widely used since its publication by Yodzis & Innes (1992), and has led to major advances in ecology (Williams et al. 2007). Its adaptation to food webs has shed new lights on various ecological puzzles, such as the complexity-stability relationship, or the generality of the BEF relationship in food webs. One of the main goals of this thesis is to show its power as a synthesis framework for the analysis of factors influencing the functioning of complex ecological communities, especially when combined with food web analyses.

By explicitly using concepts from diverging fields of ecology, results from chapter 4 show that there is an interplay between food web structure and energetic constraints, captured by characteristic shapes of biomass distribution.The majority of communities are, in nature as in our analysis, bottom heavy (Bar-On et al. 2018). This is consistent with theoretical predictions from the literature: in the absence of external input (subsidies), because of the distribution of body sizes in the community, imperfect assimilation and metabolism, it is energetically difficult to maintain top-heavy communities (McCauley et al. 2018). And we show that these "default" communities display little variability in food-chain length and animal diversity. In the context of our analysis, they often have high plant diversity, and a low animal to producer ratio. The positive diversity-functioning relationship we see in these communities is mainly driven by plant diversity, but greater animal diversity can increase the general level of functioning of the system, independently of food-chain length (which is often limited to 3 trophic levels). Within the BEFWm, these "green" communities are in the majority of cases less efficient at storing the material produced by heterotrophs than equivalent grasslands (i.e., with equal productivity).This shows that in this case, the addition of consumption (and the subsequent consumption losses) may prevent competitive exclusion among producers (Brose 2008), potentially increasing diversity, but also seems to decrease the effect of diversity

Rarely, top-heavy communities can exist and persist. Food-web analysis sheds new light on the conditions for their emergence. Previous results have shown the role of omnivory and intraguild predation - which structurally translate into the same motif $A \rightarrow B \rightarrow C \leftarrow A$ - in attenuating the trophic cascade and stabilizing biomass dynamics (Finke & Denno 2004, 2005). The frequency of intraguild predation (IGP) is also correlated with higher food-web functioning and greater diversity (Wang et al. 2019). The use of motifs frequency to measure the structure of food webs (as established in chapter 3) allows us to link these results (chapter 4). Specifically, we show that communities with a high animal diversity and a high animal to producer ratio have a more complex structure (represented by a relatively higher connectivity) and more omnivore/IGP motifs. These communities are also more efficient at storing the biomass produced (slower biomass turnover), and can even be more efficient than grasslands at equivalent intake. This energy efficiency is linked to a higher consumer-resource body-mass ratio on average (because predators feed on different levels of the food chain), which is associated with higher stability and lower consumption and metabolic losses.This appears to be the reason for their top-heavy structure.

5.2 Reconciling predictions from food-chain and BEF theories

The analysis of food chains functioning, of isolated trophic compartments functioning (usually framed in BEF analyses), and of the influence of the trophic cascade phenomenon on BEF relationships has given us some fundamental building blocks that allow us to better understand the functioning of the communities. However, the simplicity of the systems generally used to perform these analyses is not representative of the complexity of the realistic communities. It was therefore necessary to test the generality of these predictions, their range of applicability and their influence on each other in more realistic systems. We have tried to answer the following questions in realistic food webs: Under what condition can we produce top- and bottom-heavy food webs? Is there a correlation between diversity and functioning in complex food webs? Is the effect of chain length on the diversity-functioning relationship independent of the structure of the network? What is the effect of the omnivory and IGP on the emergence of these results? We answer these questions usingan efficient, tractable and empirically grounded model: the bioenergetic model for food webs.

Top heaviness in the bioenergetic food-web model framework. The emergence of top-heavy communities, and especially inverted pyramids of biomass, has long puzzled ecologists. It has been later shown that subsidies – external inputs into the community – can lead to top-heavy communities, as well as efficient energy channels that enhance biomass transfers between trophic compartments (McCauley et al. 2018). In the context of the experiments presented in chapter 4, we show that top-heavy communities (but rarely inverted pyramids) are theoretically possible without exogenous energy input. They appear into communities displaying a densely connected food-web, with a strong consumer-resource body-mass ratio and lead to highly functioning systems. However, while our results are consistent with Trebilco et al. (2016) given the parameters value in the BEFWm, it could also be interpreted as an overestimation of the transfer efficiency parameters in the BEFWm. More empirical and experimental work in establishing these parameters is needed to test the validity of our results.

The BEF relationships in complex ecological communities. Coupling a food-web model generating realistic communities (ADBm; Petchey et al. 2008a), and the BEFWm, we see a positive asymptotic relationship between diversity and functioning in complex communities. Consistently with previous work (Schneider et al. 2016; Wang & Brose 2017; Wang et al. 2019), diversity effects in complex communities are not as idiosyncratic and dependant on structure as previously thought (Thébault & Loreau 2006; Loreau 2010a). Rare complex, rich in animal and top-heavy communities do present a higher level of functioning for similar species richness levels, but qualitatively, the diversity-functioning relationship is similar for all types of food webs analyzed. Interestingly, BEF relationships in food webs, in the context of our analysis, appear to logically follow from the synergy of structural and energetic constraints. More diverse food webs are correlated here with higher animal richness and complexity. Because many food webs in nature have a positive consumer-resource body-mass ratio, and following the allometric scaling of biological rates in our model (especially maximum consumption and metabolism), consumption losses and metabolism are lower in these food webs. They also have statistically more omnivory motifs. It naturally follows that they have i) a higher productivity and ii) a lower turnover rate. This means that they are bound to be more efficient at producing and storing biomass.

Effects of food chain length and omnivory in complex ecological communities. In simple community food chain, the number of discrete trophic levels (food-chain length) explains the distribution of biomass in trophic compartments through trophic control. In systems with strong top-down trophic cascade, an even number of trophic levels result in a release of herbivores and a strong control of producers. Omnivory, by dampening the trophic cascade, can alter this prediction. Here, it appears that we see the result of this phenomenon. One the one hand, most communities are relatively simple and bottom heavy. In these communities, food-chain length only varies in the $]1, 3.5]$ range, and is mainly below 2, showing that secondary consumers in these communities are often omnivores, feeding on both producers and consumers. The presence of omnivory and the narrow range of variation in food-chain length make it difficult to analyze its potential effect. On the other hand, more complex top-heavy communities do present a wider range of variation, but the high frequency of omnivory and intraguild predation probably strongly suppresses the effect of the trophic cascade. As a consequence, in the context of our methodological framework, we did not see an effect of food-chain length.

5.3 Perspectives

5.3.1 Realistic scenarios of secondary extinctions and adaptive foraging

The global changes we are facing — and causing — considerably threatens biodiversity and we see novel ecological communities emerging, with changed composition and structure (MEA 2005). Current extinction rates are comparable to the great biodiversity crises that punctuated the history of life on Earth (Barnosky et al. 2011) and invasion by exotic species is an increasingly frequent phenomenon (MEA 2005). As species exist not alone but in a web of interactions with various others, extinction or invasion events are more than likely to be followed by a cascade of consequences. These consequences are diverse and range from changes in species behaviour (to avoid a new predator or adapt to a new resource), density and persistence in the community. Predicting the cascading consequences of primary extinctions or invasions requires that we understand the factors driving them, and the subsequent changes in food web structure and processes.

Species extinction risk and invasion success are correlated to certain traits. For example, we know that large predators are disproportionately vulnerable to extinction (Cardillo 2003). Specialists are also at greater risk, as they have a narrower range of possible adaptation if their resource disappears (Brodie et al. 2014; Gallagher et al. 2014, 2015). Beyond improving management and conservation efforts, this knowledge also provides realistic targets to simulate primary extinctions and their consequences in model systems (Srinivasan et al. 2007). Conversely, analyses of secondary extinctions (Ebenman et al. 2004) can also provide us with a better understanding of the correlation between species traits, structural properties and extinction risks (e.g., Petchey et al. 2008c; Allesina & Bodini 2004; Roopnarine 2006; Brodie et al. 2014). This type of analysis is relatively common and provides valuable insights in the fate of ecosystems (Estes et al. 2011). However, we also know that changes in biomass are an early warning of species extinction (before disappearing, species abundance necessarily drops significantly, leading species to become "functionally extinct"; Säterberg et al. 2013; Anderson et al. 2011). Consequently, many species are the subject of short-term fluctuation in diet that allows them to adapt to these changes (Stephens & Krebs 1986; Agrawal 2001). Adaptive foraging has been documented in nature, consumers for example can switch their diet to respond to changes in resource availability or energetic value (Agrawal et al. 1999), causing a rewiring of the food web. When adaptive foraging has been integrated with models of biomass dynamics in food webs, it showed that rewiring generally stabilizes biomass dynamics and decreases the number of secondary extinctions following a primary extinction event (Kondoh 2003; Roopnarine 2006; Staniczenko et al. 2010; but see Gilljam et al. 2015). Research focusing on the mechanisms of adaptive foraging and their consequences on stability has produced many interesting insights, but little is known about their consequences on community processes.

Various models of adaptive foraging have been developed recently (see for example Staniczenko et al. 2010; Gilljam et al. 2015). After publication of the `BioEnergeticFoodWeb.jl` package, we implemented in version 1.0 (Delmas et al. 2019b) some of these models, the diet overlap (Staniczenko et al. 2010), diet similarity (Gilljam et al. 2015) and adapted the allometric diet breadth models (Petchey et al. 2008a) to simulate adaptive foraging and trophic rewiring. This gives new potential to the `BioEnergeticFoodWeb.jl` package to simulate biomass dynamics in food webs under different mechanisms of foraging adaptation, which have so far resulted in opposite predictions (Staniczenko et al. 2010; Gilljam et al. 2015). The publication of this new feature makes it easy to (i) investigate the consequences of realistic targeted extinctions on biomass dynamics, diversity, functioning and food web structure, but also to (ii) compare the consequences of various mechanisms of rewiring.

5.3.2 From organisms to ecosystems

If we are interested in predicting community functioning, it is ultimately to predict the fate of ecosystems, their functioning and of the multiple services they provide to human societies (Balvanera et al. 2006; Haines-Young & Potschin 2010). Scaling up our results from communities to ecosystems would require that we include the effect of environment on the ecological processes of interest, at different organizational, temporal and spatial scales. Here we highlight some interesting future avenues for research in this direction, and their potential influence on the relationships as shown in chapter 4.

Communities rarely, if ever, exist in isolation, they are connected to a web of others through dispersion, migration, and energy and matter fluxes. This has the potential to change the relationships we highlight in chapter 4 in various ways. At the most basal level of our analysis, nutrient inflow (fertilization) into the community could have different consequences. These consequences could easily be analyzed by manipulating the supply rate of the nutrient-intake model for producers growth that we included in version 1.0 (Delmas et al. 2019b) of `BioEnergeticFoodWeb.jl` . While increasing nutrient supply could allow maintaining more species and trophic levels, allowing for higher predators in the food chain (Post 2002), the paradox of enrichment (Rosenzweig 1971) tells us that it could also destabilize biomass dynamics and potentially cause extinctions. Subsidies have also been shown to increase the probability of top-heavy communities (McCauley et al. 2018). Higher in the food chain, source-sink dynamics have the potential to change the food web structure and function (Loreau et al. 2003; Grace et al. 2016), not only by changing biomass dynamics between compartments, but also because of changes in behaviour (e.g., avoidance of abundant predators) and diet preference. Integrating meta-community processes with adaptive foraging models in a bioenergetic framework has the potential to change in unpredictable ways how we understand the effect of food-web structure on the diversity-functioning relationship. It could notably make it easier for top-heavy communities to emerge and persist, thus potentially causing shifts in the functioning regime of communities.

Working at the regional scale would also allow us to understand the consequences of diversity change at different scales. While it is an established fact that global biodiversity is decreasing dramatically (MEA 2005), the effects are not the same at the global, regional and local scales (Sax & Gaines 2003). In fact, it appears that local (alpha) diversity is not affected as much as previously thought, while regional diversity, the pool of species from which local communities are assembled, is more negatively affected. This makes communities more homogeneous (smaller beta diversity) and in turn reduces the potential for compositional turnover. Beyond species, interactions can vary in response to environmental factors and neutral processes (Poisot et al. 2015c). The bioenergetic framework includes the possibility to account for some species traits (mainly body mass and metabolic class so far) that are important in estimating energetic demands and food web structure. This makes it an adapted framework to study how a decrease in regional functional diversity would in turn affect local processes and food web structure.

In a more and more fragmented and altered world, analyzing the effect of environmental variations, at different scales, is also a necessary stepping stone. Temperature for example, can influence communities by changing organisms biological rates, body sizes and the resulting ecological processes (Gillooly et al. 2001; Brown et al. 2004; Walters & Hassall 2006). Fertilization, as we stated just above, is another source of concern, as many ecosystems face this type of perturbation. In fact, ecological communities face a variety of simultaneous stressors that enter systems at different levels and act at different scales, from individual organisms to the whole ecosystem, and affect different ecological mechanisms (Orr et al.

2020). To this date studies that have focused on investigating the simultaneous effects of these factors have done so in simplified systems and only included few stressors (Kéfi et al. 2019). The results, however, highlight the importance of this issue, as they show how the interactive effect of as little as two stressors (temperature and fertilization, for example; Binzer et al. 2012) can have counteractive effect on stability and functioning. To move forward in this direction, in version 1.0 (Delmas et al. 2019b) of `BioEnergeticFoodWebs.jl` , we have implemented models of temperature effect on both biological rates and body size, and are moving on to include other potential stressors effects. Building a statistical framework to understand the additive or interactive effect of many stressors, that exert simultaneous press or pulse perturbations, at various scales will also be of primary importance to build a predictive framework for biodiversity and ecosystem functioning for different scenarios of perturbation, and in heterogeneous environments. Developing the `BioEnergeticFoodWeb.jl` platform to include effects of various stressors, meta-community dynamics and developing the statistical framework to analyze the effect of simultaneous, heterogeneous stressors will in fact be part of my new research focuses as a postdoctoral research assistant.

5.3.3 Network analysis offers many perspectives to solve these complex issues

Networks occur at all scales of ecosystems, connecting species, individuals, habitats, ecosystems. The development of network analysis has provided new ways to abstract complex systems and study their dynamics in various fields. In ecology, network analysis is more and more used to analyze various problems (Proulx et al. 2005). In the context of this work — and many other that focus on biodiversity and community functioning — representing communities by their underlying maps of energy and matter flow (food web) has provided many insights (Pascual & Dunne 2005), whether it adopted a static (steady state) or dynamic vision of communities. However, this is still a relatively recent field and new developments are needed, especially in two areas: comparing of ecological networks and analyzing multilayered networks (Delmas et al. 2019a).

Comparing networks presents a unique challenge, depending on whether networks contain similar sets of species or not. However, it has the potential to provide valuable results, for example by linking variations in structure, diversity, environment and functioning, at different scales. To date, network comparisons have been mainly done using multivariate analyses of a set of metrics (Vermaat et al. 2009), describing structure (mean and standard deviation in degree, connectance, etc). More comprehensive metrics (such as motifs distribution; Milo 2002) provides us with new insights, but as many different structural properties are correlated to connectance and size (Dunne et al. 2002a), this type of analysis has its limits. To capture the multivariate reality of ecological networks, we need more comprehensive metrics. Mainly, this type of approach could help us studying empirically the effect of environmental gradients on the structure of networks, which in turn would help test the validity of theoretical predictions based on the use of the bioenergetic food web model. Notably, a recent method based on the alignment of ecological networks using on their motifs holds great promise for measuring network dissimilarity (Mora et al. 2018b) and has been used to show the existence of a "backbone" of interactions in food webs. Comparing the different local realization of the same regional pool of species can also be done by estimating pairwise network dissimilarity (Poisot et al. 2012). Using these approaches, we could test whether food web dissimilarity and variations in functioning are correlated. This would be a big step towards reconciling biogeography and food-web analysis, and understanding the BEF relationships along environmental gradients.

Ecosystems are, as Schmitz (2010) put it "paradigmatically one of the most complex systems known to science." They are composed of many species that display a wide variety of traits and that interact with one another — and with one another environment — through a myriad of interactions. The work presented in this thesis, as many before, focuses on consumption, and to a certain limit, competition. But pollination, facilitation, parasitism, etc. are more than likely to change the effect of competition and consumption that we are able to measure (Fontaine et al. 2011b). The analysis of networks with different types of interactions is still in its early stages, especially in ecology, but has already shown that including non-trophic interactions modifies the effect of biodiversity on biomass (Arditi et al. 2005; Goudard & Loreau 2008; Kéfi et al. 2012). The integration of BEF analysis in food webs was born from the realization that consumption was probably changing the strength and effect of competition between species within a trophic compartment (Duffy et al. 2007). Food webs provided a framework to integrate both competition and consumption and host the subsequent analyses (Loreau 2010a). If we want to move towards more accurate predictions, we need to test the influence of other interactions through the development of integrative frameworks able to abstract the complex reality of ecosystems with many interactions.

5.4 Conclusion

With the publication of a common open platform for the bioenergetic food-web model, we are making it easier to integrate various existing models, simulating processes such as adaptive foraging or temperature effect, in a tractable but realistic framework. This platform offers the possibility for rapid development in our ability to understand and predict community dynamics. We show that the coupling between this model and the new developments in ecological networks analysis provides a powerful framework to solve many exciting new challenges.

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