University of Namur

DOCTOR OF SCIENCES

Reinterpretation of niche and fitness differences improves our understanding of species coexistence

Spaak, Jurg

Award date:
2020

Awarding institution:
University of Namur

Reinterpretation of niche and fitness differences improves our understanding of species coexistence

Jurg W. Spaak

Acknowledgements

While this thesis goes under my name and I’m proud of my work, many people sustained my work.

My first round of thanks goes to my family. To my wife Jenny, who believed in me and calmly listens to my new findings even when she doesn’t understand or care about them. Most importantly, you convinced me to apply for this PhD position, despite my mathematic background. There are so many more thanks to you, but those are private and not public. To my kids NORA, JOHANNA and ARTHUR (who cannot read lower case letters yet): Für wenn ihr mit mir dur d Uni gloffe sind, mit mir sind cho go schaffe und für jedes mal wo ihr mich diheime hend la schaffe, obwohl ihr hend mit mir welle spiele. Nehmed das Buech und macheds zu euerem. A special thanks goes to my father Maurus, with whom I discussed many of my findings and who asked the most critiquing questions about niche and fitness differences. To my father-in-law Piet, who helped me understand how academia works and for forcing himself to read my papers, despite the high level of mathematics. I also want to thank the rest of my family and everybody who ever came to visit us in Belgium to bring us some Switzerland.

The second round goes to my collaborators from Namur. Most of all, to you Frederik, my supervisor. You put much faith in me from the start and gave me a lot of freedom, which I enjoyed very much. You listened to my enthusiasm and supported me. The most angry you ever got at me (when I screwed up quite a bit) was: ”I really don’t like that very much”. Thank you for supporting me, both as a person and as a scientist. To Marie who taught me lab work. I started as a pure theoretician with no understanding of experiments. Now I’m a pure theoretician who understands that experiments are hard. To Julie, who protected my cyanobacteria from extinction. To Camille and Mark, with whom I shared many funny hours in and out of office. Also for taking mathematical advice from me and making me feel smart. And to my mentees, Elif, Stan, Remi and Lisa. Thanks again for all the work you have done for and with me. And sorry for all the times I was an insufficient supervisor myself.

The next round goes to my other collaborators. Francesco, you accommo-

dated me for the first year of my PhD. You taught me, that science is not only serious, but also a lot of fun and goofing around. Every time I visited your lab I felt very welcome. To Oscar and Gyuri, you were the first scientists who showed interest in my work and gave me confidence that my work is important. And to my co-authors, Andrew and Po-Ju, for taking my questions seriously.

Finally, to God. You have created this entire world with its mysteries for us to study it, marvel at it and see you through the beauty of your works. You have guided me on my path so far and will guide me further. Thank you for hearing all my prayers. And forgive me for all the times I failed to acknowledge you so far.

Contents

Chapter 1

Introduction

1.1 What is (modern) coexistence theory?

1.1.1 What does (modern) coexistence theory investigate?

Coexistence theory, including modern coexistence theory (MCT), aims to understand, explain, and predict the persistence of species observed in nature. Coexistence theory assumes that the species diversity observed in nature is not a mere co-occurrence, but rather that at least some species coexist. That is, it assumes that the species densities do not follow a long term trend, but rather that they have a stable distribution, i.e. species do not go extinct. It also implicitly assumes that the environmental conditions, similar to species densities, may follow short-term fluctuations, either periodically or chaotically, but do not follow long term trends either.

Coexistence theory does not explain the global species pool via speciation, or how regional species pools arise via environmental filtering or dispersal, but takes species pool diversity as a given. Generally, it used to ask the question: out of the species currently present locally, which species combination will persist indefinitely? Few papers, however, investigate how evolutionary adaptations in species traits can affect species persistence (Hart *et al.*, 2019).

Coexistence theory is typically applied to species from the same guild. The term guild is not defined precisely, rather it is a term that is understood intuitively. Roughly, the term describes species that are limited by the same limiting factors and occupy similar niches. Examples of guilds are species from the same trophic level; phytoplankton competing for nutrients and light; terrestrial plants; consumers; or top predators. Species can be from the same guild, yet have completely different phylogeny, e.g. cyanobacteria and algae typically belong to the same guild. Coexistence theory is usually applied at the species level, but could just as well be applied to the family or subspecies level.

As species belonging to the same guild they compete for common resources and therefore interspecific interactions are predominantly negative. However, species from the same guild can also interact positively, e.g. by facilitating each other directly or via common mutualists (Johnson & Bronstein, 2019). Coexistence theory rarely focuses on entire foodwebs, rather it focuses on one specific trophic level within a foodweb and explains how diversity within this trophic level is maintained, assuming that species from other trophic levels cannot go extinct (Chesson & Kuang, 2008). However, recent advancements are changing this restriction of coexistence theory to include facilitative interactions (Bimler *et al.*, 2018; Spaak & De Laender, 2020) and focus on entire foodwebs (Godoy *et al.*, 2018; Serván *et al.*, 2018).

1.1.2 What is modern coexistence theory?

Given this focus of coexistence theory, there are many different community models to be analysed (Lawton, 1999). Sub-branches have emerged that have investigated in detail the possible outcomes of species interactions, most notably resource competition theory (Tilman, 1982) and Lotka-Volterra models (Lotka, 1920; Gause, 1934; Volterra, 1926). While these sub-branches lead to a detail understanding of the given community models, they usually lack general community-independent insights. In contrast, MCT does not focus on any specific community model, but proposes a framework with which a large class of communities model can be analysed in a unified way. To do so, MCT breaks down all mechanisms at play into two groups of mechanisms, stabilizing/equalizing mechanisms, and niche/fitness differences (Chesson, 2000), which are discussed below in more detail.

This generality is achieved with invasion analysis. To assess whether all species of a community coexist, one sets the density of the focal species to zero and tests whether this focal species can recover. If all species can invade, the species are assumed to coexist. Decomposing the invasion growth rates into various parts gives insight into why species coexist.

Invasion analysis is both the key advantage of MCT as well as its major drawback. For any community in which invasion analysis correctly predicts coexistence, MCT can decompose the invasion growth rates to understand why species coexist. This leads to a very general theory, but one that is of no use for any community for which the inavsion growth rates do not correctly predict coexistence (Barabás *et al.*, 2018; Grilli *et al.*, 2017; Schreiber *et al.*, 2019)

The defining papers of MCT are: Chesson (2000), which is arguably the founding paper of MCT and introduces the concepts of stabilizing and equalizing mechanisms and how they can be used to understand coexistence. Adler *et al.* (2007) explains how niche and fitness differences can be used to unify neutral theory (Hubbell, 2001) with modern coexistence theory, as neutral theory is the special case where both niche and fitness differences are absent. HilleRisLambers *et al.* (2012) integrates niche and fitness differences into community assembly and review which experiments have manipulated niche or fitness differences. Barabás *et al.* (2018) reviews, and to some extent reinterprets, Chesson's coexistence theory based on temporal and spatial fluctuations.

1.1.3 How modern coexistence theory relates to other fields of community ecology

MCT investigates indefinite persistence of species, i.e. whether the community return to the same community after a given perturbation?

MCT typically considers perturbations that affect species densities and not the environmental conditions or species traits, it therefore differs from structural stability analysis (Saavedra *et al.*, 2017). The invasion criterion formalizes the perturbation of the species densities (Turelli, 1978). The perturbation may be arbitrarily large, it therefore differs from local dynamical stability analysis (May, 1972; Allesina & Tang, 2012, 2015). MCT does not focus on transient states, it therefore differs from ecological stability research that focusses on resilience and recovery times (Radchuk *et al.*, 2019).

Naturally, however, there are many links to other fields in ecology. For example, niche differences describe how much species differ in their resource requirements. Therefore, species with large niche differences should harvest more of the available resources and consequently have higher ecosystem function (Turnbull *et al.*, 2013; Carroll *et al.*, 2011; Loreau, 2004). This is one possible explanation why species or trait rich communities are associated with higher ecosystem functioning (Striebel *et al.*, 2009; Grace *et al.*, 2016; Tilman *et al.*, 2014). Similarly, species with large niche differences will be buffered against extinction, therefore they should be more stable against perturbations (Adler *et al.*, 2007). MCT predominantly investigates the stability of a community model, i.e. does the community return to its equilibrium after a perturbation of species densities. Alternatively, structural stability research investigates whether the system remains stable after a perturbation of species parameters (Meszéna *et al.*, 2006; Saavedra *et al.*, 2017; Song *et al.*, 2020b). Finally, while MCT focuses on the coexistence of species within one guild, other fields focus on the coexistence of antagonistic networks (May, 1972; Allesina & Tang, 2012).

1.2 Historical overview of (modern) coexistence theory

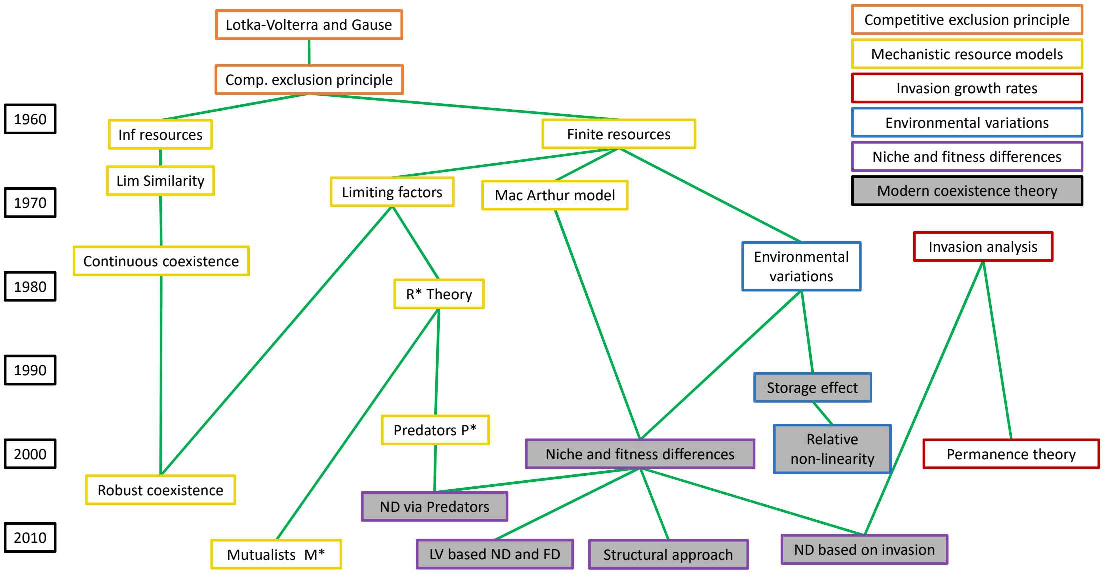

Figure 1.1: Historical overview of (modern) coexistence theory. The boxes represent key contributions of coexistence theory, sometimes they denote the founding ideas (e.g. Invasion analysis), sometimes they denote important reviews (e.g. R^*). The colours group the contributions and correspond to the subsections 1.2.1-1.2.5. The key concepts of MCT are shaded grey. The edges denote loosely how the contributions are based on each other. Simplicity was prioritized over completeness, for example R^* theory was mentioned in most later contributions, similarly, robust coexistence cites most previous contributions.

In this section I want to discuss how coexistence theory has evolved over time. However, the advancements of coexistence theory will be grouped thematically and not strictly historically for better overview. Within one branch of coexistence theory I will try to follow the historical course more closely. The representation chosen here does not necessarily represent how important the sub-branches or advancements are for science in general, rather I highlight which papers paved the way for MCT and more specifically for my research focus during my PhD. Figure 1.1 gives a graphic overview of coexistence theory as well as of this section.

1.2.1 The competitive exclusion principle

Coexistence theory is a sub-branch of theoretical population ecology, which starts with the Lotka-Volterra model (Lotka, 1920; Volterra, 1926; Kingsland, 2015). Lotka originally used the model to describe the densities of two species, a predator and a prey, which lead to periodic oscillations of species densities. Volterra derived the same equations independently from Lotka explaining the number of fish caught during World War One (Kingsland, 1995; Volterra, 1926). The model has henceforth been used to describe many different community types, including plant communities (Keddy & Shipley, 1989), multispecies communities (Serván *et al.*, 2018), environmental changes (Spaak *et al.*, 2017) and many others. There are multiple equivalent ways to formulate the Lotka-Volterra model (LV). The most often used in coexistence theory are:

$$\begin{aligned} \frac{1}{N_i}\frac{dN_i}{dt} &= \mu_i - \mathbf{A}N \qquad (1.1) \\ &= r_i(1 - \mathbf{A}'N), \qquad (1.2) \end{aligned}$$

where N_i is the density and μ_i is the intrinsic growth rate of species i. Throughout this thesis we assume that i is the index of the focal species and j is the index of the non-focal species. In a multispecies community j will be used as a running variable, not however in a two species case. $\mathbf{A}$ is the species interaction matrix. Normalizing for species densities in monoculture leads to equation 1.2, where $\mathbf{A}'_{\mathbf{ij}} = \mathbf{A}_{\mathbf{ij}}/\mu_i$ is the normalized species interaction matrix. The parameter $r_i = \mu_i$ describes how fast species reach equilibrium. However, MCT usually does not focus on transient states, therefore r_i is usually not included into the analysis (Chesson, 1990).

The competitive exclusion principle states that, "Complete competitors cannot coexist" (Gause, 1934; Hardin, 1960). That is for species to coexist they must differ at least in some aspect regarding their niches. The competitive exclusion principle has arisen to a sort of tautology or circular argument. That is, given two species can coexist we deduce, using the competitive exclusion principle, that they must differ in some sort (Hardin, 1960; Levin, 1970).

The competitive exclusion principle could be understood as a minimal necessary condition for coexistence and is by no means sufficient. It focuses solely on the niche requirement, but it ignores potential differences in the competitive ability of species. More generally, two coexisting species must limit themselves more than they limit their competitor, i.e. $\alpha_{ij} < \alpha_{jj}$ and $\alpha_{ji} < \alpha_{ii}$. This insight is much more general than the LV model and is the fundament of MCT (see below).

1.2.2 Mechanistic resource models

LV models are phenomenological, meaning that they assume that species interact via **A**, however, no specific description for this interaction is given. There are many potential underlying mechanisms, most prominently including competition for nutrients (Tilman, 1982) or prey (MacArthur, 1970), competition for other resources, limitation via common predators (Chesson & Kuang, 2008; Holt *et al.*, 1994) or limitation via common mutualists (Johnson & Bronstein, 2019). Theoretical ecology assumes that differential equations are useful to understand community dynamics, i.e. assuming $\frac{1}{N_i}\frac{dN_i}{dt} = f(\mathbf{N})$ will help our understanding of ecology. The LV model should be seen as a Taylor approximation of the "real" underlying community model $f(\mathbf{N}) \approx \mu_i - \mathbf{AN}$ around the equilibrium or any alternative linear approximation of the underlying community model.

The LV model implicitly assumes that the interaction matrix **A** is time and density independent, which is a simplification of nature (Abrams, 1983; Letten & Stouffer, 2019).

In contrast to this are the mechanistic models, which explicitly model how species interact via other entities. The focal species do not usually interact directly with other focal species in mechanistic models, rather all species interactions are indirect via other entities. However, "mechanistic" should be seen as a relative term. For example, the Tilman resource models are clearly more mechanistic than LV models, yet they do not mechanistically explain how the species traits, such as half-saturation constants, arise mechanistically from the species morphology or genes. The entities in these mechanistic models are usually called limiting factors. I will assume that it is intuitively clear what a limiting factor is and refer to Levin (1970) for their precise mathematical definition.

Two conceptually different mechanistic models are possible, models with a finite number of resources (or more generally limiting factors) and models with an infinite number, usually a continuum, of resources.

Finite number of limiting factors

The competitive exclusion principle applied to a mechanistic model with only one resource or limiting factor implies that only one species can survive, as there is only one possible niche and species must be complete competitors (but see 1.2.4). This notion has been generalised, the number of coexisting species is limited by the number of resources (MacArthur & Levins, 1964) and even more generally the number of limiting factors (Levin, 1970).

Most attention has been given to the case of species competing for resources, most notably to two species competing for two resources, as it is the simplest non-trivial example. Tilman (1982) reviews the available literature and coined the so-called R^* theory. R^* is the resource concentration at which a species has zero net growth rate. Resource concentration above R^* leads to a positive growth, while resource concentration below R^* leads to a decline of species densities. If multiple species compete for one resource, the species with the lowest R^* will competitively exclude all others, as it will draw down resource concentrations to its R^*, at which point all other species have negative growth.

Conversely, two species competing for two resources may coexist if there is a trade-off between their R^*. That is the species with a lower R^* for the first resource must have a higher R^* for the second resource. Similar results have been found for species limited by predators and mutualists, leading to a P^* and M^* theory respectively (Johnson & Bronstein, 2019; Holt *et al.*, 1994). However, a trade-off in the R^* is again only a necessary condition for coexistence, not sufficient. The species will coexist when they consume more of their most limiting resource, otherwise priority effects or competitive exclusion emerge (Ke & Letten, 2018).

In general, the number of limiting factors must be larger than the number of coexisting species. However, this holds true only when the species coexist at fixed densities (see 1.2.4).

That the number of limiting factors must exceed the number of coexisting species has led to the ″paradox of the plankton“ (Hutchinson, 1959). Phytoplankton species are thought to be limited by only few resources, most notably phosphorus, nitrogen, and light. Yet even small samples of lake or seawater typically contain more than 50 different phytoplankton species, vastly exceeding the number of limiting factors. This paradox has inspired a generation of scientists to search for potential solutions, including partitioning of the light wavelengths (Stomp *et al.*, 2004), internal fluctuations of resource concentrations (Huisman & Weissing, 1999), and environmental fluctuations (see 1.2.4).

Infinite number of limiting factors

A qualitatively different case is when the number of limiting factors is infinite, most often assumed to be a continuum. This is biologically meaningful if we assume, for example, birds competing for a tree's seeds. The seeds produced by the tree will not all be identical, but vary in a certain trait, e.g. size Roughgarden (1979). Similarly, one could imagine a continuum of predators as limiting factors that slightly differ in their consumption preferences. However, predators and resource function in a very similar way as limiting factors in the case of finite limiting resources (Chesson & Kuang, 2008), this suggests that investigating a case with a continuum of predators will not reveal fundamentally new insights. The infinite resources are usually assumed to be one dimensional. However, one could also use resource continuum in higher dimensions. As the number of limiting resources is infinite, the insights gained from the finite limiting factors is of little use.

First investigations on the infinite resource models suggested that species are limited by their similarity, which became known as "limiting similarity“ (MacArthur, 1970). For this, species are defined by a niche location, the resource they consume most, and a niche width, the standard deviation of the resource consumption vector. They found that the distance between the niche location (defined as the maximum of the consumption vector) of coexisting species is proportional to the niche width (defined as the variance of the consumption vector). More generally, limiting similarity has been interpreted to mean that even a continuum of resources will not lead to a continuum of coexisting species, as there is a limit to how similar two species can be.

Later works included the possibility that species evolve (Case, 1981; Roughgarden, 1976), that species differ in their niche width (**?**) or that species differ in their total resource consumption (Taper & Case, 1985). All these confirmed the expectation of a limit to similarity.

A famous counterexample was given by Roughgarden (1979), where indeed a continuum of species coexist on a continuum of resources. Other examples of community models that are not limited by similarity have been found as well, implying that the stable coexistence of a continuum of species may indeed be possible and there's no lower limit to similarity (Abrams, 1983). Yet, the idea of a continuum of coexisting species was rejected for two reasons. First, we never observe this in nature. Second, it was assumed that the existence of this continuum of coexisting species was only possible, because the underlying resource model was very simplistic and not close to nature (Barabás *et al.*, 2012).

Robust coexistence

Meszéna *et al.* (2006) unified community models using both finite or infinite numbers of limiting factors. To do so, they introduce the impact and sensitivity niche, which describe how much a species affects limiting factors and how much a species growth rates are sensitive to changes in limiting factors, respectively. The impact and sensitivity niches are vectors or functions for the finite limiting factors and infinite limiting factors case, respectively.

Furthermore, they introduce the concept of structural stability, in addition to dynamical stability. Structural stability measures how much the community parameters can be changed before coexistence is lost. The structural stability of a community is a product of the impact and the sensitivity niche. Species from a structurally stable community must therefore differ in both their impact and sensitivity niche.

Limiting similarity implies that the structural stability tends to zero as species become more and more similar. Consequently, the Roughgarden example is dynamically stable, but not structurally stable, any tiny perturbation of the species intrinsic growth rates destroys the continuous coexistence. This result applies more generally to a large range of possible community models as reviewed by Barabás *et al.* (2012).

Linked to structural stability is the evolutionary stability. An equilibrium is evolutionary stable, if no species can increase their growth rate by evolving their traits (Edwards *et al.*, 2018). In general, evolutionary stable equilibria are more stringent and less species rich (Edwards *et al.*, 2018). But evolutionary stable equilibria show similar features as their stable counterparts, such as a limiting similarity (Kremer & Klausmeier, 2017).

1.2.3 Invasion growth rates

Communities with environmental fluctuations will never stay at a stable equilibrium, which makes it much more difficult to assess coexistence. Therefore, a species is said to persist if its densities are bounded away from zero to below infinity (Schreiber, 2000). This notion, however, is only used conceptually, as it is hard to assess this empirically. Therefore the more pragmatic approach of invasion growth rates is used.

The invasion growth rate of an invading species i (called invader) is its growth rate at low density (effectively zero) when the resident community (called residents) is at an equilibrium density distribution (Turelli, 1978). The existence of such stable equilibria is, however, disputed as many systems show chaotic behaviour (Benincá *et al.*, 2008; **?**). If all species have positive invasion growth rates, then all species are assumed to coexist. This condition is equivalent to the positive boundedness criterium for some communities.

However, we know of examples where the invasion growth rate does not correctly predict the outcome of species interactions or where invasion analysis is not applicable (Barabás *et al.*, 2018). A crucial assumption is that the resident community will be able to coexist at a stable equilibrium, and there exist famous counterexamples such as the rock-paper-scissor community (Grilli *et al.*, 2017) or food webs, where the higher trophic levels are not viable without their prey. Additionally, Pande *et al.* (2019) have shown that the invasion growth rate only captures qualitative information about coexistence, not quantitative information, as species with higher invasion growth rates do not necessarily have a higher probability of invasion success.

Schreiber (2000) and Patel & Schreiber (2018) have proposed generalised invasion growth rates, along with conditions under which they correctly predict coexistence. However, these are rarely applied empirically, because they, again, depend on analytical mathematics.

Despite their theoretical limitations, invasion growth rates remain used very widely (Letten *et al.*, 2018; Carroll *et al.*, 2011; Narwani *et al.*, 2013; Zepeda & Martorell, 2019). Grainger *et al.* (2019b) proposed the invasion growth rates as a common unit to compare different communities (despite Pande *et al.* (2019)). This would broaden the applications of invasion growth rates beyond MCT to many other applications of ecology.

1.2.4 Environmental fluctuations

Most of the results found on the competitive exclusion principle assumed that the species must coexist at fixed densities. Without this assumption, any number of species can coexist on as few as four fluctuating resources (Armstrong & Mcgehee, 1976). The community model chosen lacks biological realism and is rather a conceptual counterexample.

More realistic examples, however, showed that two species can coexist on a single fluctuating resource based on a gleaner-opportunist trade-off (Litchman & Klausmeier, 2001). The gleaner will have higher growth rates at low resource concentrations and would outcompete its competitor without environmental fluctuations. The opportunist, however, can profit from periods with high resource concentrations and accumulate enough biomass to survive lower resource concentrations. Originally, it was assumed that environmental fluctuations will always be beneficial for coexistence, as both species will have time in which they have larger growth rates than their competitor.

Chesson (1994) provided a unified framework to analyse the effect of temporal variations on species coexistence. He showed that temporal variation of the environment can be both beneficial and detrimental to species coexistence, depending on the specific model parameters. This influential work has been reinterpreted multiple times (Chesson, 2003; Barabás *et al.*, 2018; Ellner *et al.*, 2019). While the original ideas all trace back to Chesson (1994), I will explain the temporal variation as it is currently understood (as proposed by Barabás *et al.* (2018)). The (invasion) growth rate of a species can be decomposed into frequency independent effects (denoted r_i'), fluctuation independent but frequency dependent effects (denoted $\Delta\rho_i$), and fluctuation dependent effects. The latter can be decomposed further into relative non-linearity (ΔN_i) and storage effect (ΔI_i). All these effects can be beneficial or detrimental for coexistence, however, most attention has been given to cases where they promote coexistence. I will therefore explain these effects assuming they are beneficial for coexistence.

r_i' describes any differences in intrinsic growth rates that arise independent from any frequency dependence, such as higher mortality rates or higher total resource consumption rates. This factor is independent of the species density and frequency, it cannot, therefore, contribute to coexistence on its own. $\Delta\rho_i$ describes fluctuation-independent mechanisms that can arise through, for example, resource partitioning. This term does not occur in Chesson (1994), as that work specifically assumes all species are limited by only one limiting factor. Conceptually, the case with only one limiting factor is the most interesting, as fluctuation independent theory predicts that only one species can persist. ΔN_i describes how species react differently to environmental variation and captures, for example, the gleaner-opportunist trade of. It is based on Jensen's inequality, that is the average of the growth rates may not be equal to the growth rate of the average environmental condition.

ΔI_i, the storage effect, became the most investigated phenomena for coexistence under fluctuations (Ellner *et al.*, 2016; Angert *et al.*, 2009). It captures the idea that species can profit more from good environmental years when they are rare, than when they are common. We assume that species compete stronger within species rather than between species, and that a good environmental year for one species is bad for the other species. When a rare species faces a good year, then the competitor will not be very abundant and therefore, overall competition is low, therefore good years are very good. Conversely, when a rare species faces a bad year, competition may be strong, but the effect of competition is not that strong, e.g. if there are no resources to capture then strong competition doesn't matter. That is, bad years are not that bad, therefore the growth benefit from one good year may be sufficient to compensate for multiple bad years. As mentioned before, the storage effect has received the most attention, as it is assumed to be the most beneficial for coexistence (but see Letten *et al.* (2018) and Zepeda & Martorell (2019)).

Spatial variation may also affect species coexistence. Similar to temporal variation, spatial variation may be decomposed into the same effects. Additionally, spatial variation features a growth-density covariance, which can be beneficial to species coexistence if species are most dominant in patches that are beneficial to their growth. This spatial coexistence mechanism does not have any temporal analogue (Barabás *et al.*, 2018).

This decomposition of the invasion growth rate helps to understand how species coexist. r_i' is density and fluctuation independent, coexistence is therefore impossible, if all other variables are 0. Any affect that alters r_i' cannot, therefore, lead to coexistence, but only delay time until competitive exclusion. Any mechanisms that decrease differences in r_i' are called equalizing mechanisms (Chesson, 2000, 2003). Mechanisms that affect any of the other variables are called stabilizing, as they can lead to stable coexistence. Equalizing mechanisms can, however, affect coexistence in combination with stabilizing mechanisms. Equalizing mechanisms reduce differences in r_i', which reduces the necessary strength of stabilizing mechanisms to ensure coexistence.

While the theory was conceptually sound and intuitive, empirical applications remained scarce. Computation of all these parameters were based on analytical computations. For example, Angert *et al.* (2009) used a 17 page appendix to compute these for a new model. However, Ellner *et al.* (2019) proposed a numerical method to investigate the effect of environmental fluctuations on species coexistence. Their method is conceptually equivalent, but it may lead to different numerical decomposition of the invasion growth rate.

1.2.5 Niche and fitness differences

Much of coexistence theory discussed so far, such as competitive exclusion principle, limiting resources and limiting similarity, has focused mainly on the niche, but see (**?**). These could be condensed into the statement that species must differ in their niches. This argument only gives a maximum on the number of species that can coexist. It thus reflects necessary conditions, not sufficient conditions.

These arguments considered niche as a concept or a multidimensional space, and, importantly, something that cannot be empirically measured. Instead of measuring the niche itself, niche overlap (ρ) measures how much the niches of two-species overlap. Niche overlap is therefore a number, originally between 0 and 1 (as opposed to the niche itself, which is a multidimensional volume). Niche overlap originates from species that compete for resources and how much they differ in their resource consumptions (Hurlbert, 1978). Lately, literature talks about niche differences ($1 - \rho$) instead of niche overlap, however, this distinction is primarily a matter of taste.

The link between the mechanistic resource model and the phenomenological LV model by MacArthur (1970) helped to make the concept of niche overlap more tangible (Chesson, 1990). However, species do not only differ in which resources they consume, but also in how much of the resources they consume, which has been coined fitness differences. Stated in the language of niche and fitness differences, the competitive exclusion principle could be stated as niche differences must be positive, which is only a necessary condition for coexistence. The sufficient condition for coexistence is that niche differences must overcome fitness differences (Chesson, 2000).

This branch of MCT has sparked many other definitions for niche and fitness differences with a total of at least eleven different definitions. The eleven definitions can be grouped into three subgroups of niche and fitness differences (see below). More importantly, these different definitions have not only been used by theoreticians, but they have also been applied extensively by empiricists to measure niche and fitness differences.

So far, none of the eleven definitions have emerged as the golden standard (Godwin *et al.*, 2020; Spaak & De Laender, 2020). More importantly, there is little comparison between the different definitions that would allow one to select a standard in the coming future (Godwin *et al.* (2020) and chapter 3).

Stabilizing and equalizing mechanisms have also been coined for niche and fitness differences. In the absence of niche differences, species cannot coexist, similar to how species cannot coexist without relative non-linearity or storage effects. Therefore, any mechanism that reduces fitness differences is also termed equalizing, while mechanisms that increase niche differences are termed stabilizing. Recently, Song *et al.* (2019) have pointed out that the term stabilizing and equalizing mechanisms does not hold the same meaning when applied to niche and fitness differences than when applied to relative non-linearities or storage effect.

Lotka-Volterra like niche and fitness differences

The original definition of niche and fitness differences is based on the link between a mechanistic community model (MacArthur, 1970) and the phenomenological LV model (Chesson, 1990). We know what niche differences are in the mechanistic model and therefore can deduce what niche differences are in the LV model. This gives $\mathcal{N}_i = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$ and $\mathcal{F}_i = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{ji}\alpha_{jj}}}$. However, strictly speaking, the proof Chesson provides is only sufficient to define niche differences for community models that arise from an underlying MacArthur model. Chesson & Kuang (2008) extend this to species interacting via resource competition as well as via apparent competition and deduce similar formulae for niche and fitness differences.

Multiple other authors have defined niche and fitness differences for other models by reducing a community model to a LV like form (e.g. Godoy & Levine (2014); Bimler *et al.* (2018); Carroll *et al.* (2011)). These approaches are the most used in both theoretical and empirical work (Barabás *et al.*, 2018), potentially because of their simplicity but also because they were the first to be developed. Additionally, it is relatively easy to assess coexistence. I discuss the issues of this approach in more detail below in chapter 3.

All these approaches are based on the definition of Chesson (1990), they therefore inherit its limitations. The main limitation is that it is specific for two-species communities and that the definition is based on square roots of species interactions, and therefore not defined for facilitative interactions. Bimler *et al.* (2018) avoid this by first exponentiating the species interactions, thereby converting them to positive numbers. However, this comes at several costs, e.g. niche and fitness differences cannot be used to assess coexistence any longer (Bimler *et al.*, 2018).

Niche and fitness differences based on invasion growth rates

LV like approaches for niche and fitness differences assume that we know the underlying community model. Niche and fitness differences using invasion growth rates do not rely on such strong assumptions. Rather they rely on the assumption that invasion growth rates correctly predict coexistence (see 1.2.3). They all assume that invasion growth rates depend monotonically on niche differences and that variation in invasion growth rates depend monotonically on fitness differences. By reverse engineering, they can compute niche and fitness differences on invasion growth rates (Carroll *et al.*, 2011; Chesson, 2003; Zhao *et al.*, 2016; Carmel *et al.*, 2017; Spaak & De Laender, 2020; Adler *et al.*, 2007).

Special cases are the definitions of Carroll *et al.* (2011) and my own definition (Chapter 2), as they both are equivalent to the definition of Chesson (1990) on the LV community model. The definition of Carroll *et al.* (2011) has been specifically designed as such. My definition is based on independent assumptions, but it happens to lead to identical niche and fitness differences. These two independent deductions of niche and fitness differences for the LV model should be seen as evidence that both approaches are correct and that niche and fitness differences could be seen as a real phenomena.

Structural approach

The structural approach defined by Saavedra *et al.* (2017) is a completely independent approach to define niche and fitness differences. They define niche differences as the volume of all intrinsic growth rates for which the community would coexist, and they define fitness differences as the distance between the current intrinsic growth rates to the center of this set. While originally proposed as an alternative definition for niche and fitness differences (Saavedra *et al.*, 2017), it has been shown that niche and fitness differences in the traditional sense do align with these interpretations, but are not identical (Song & Saavedra, 2020). The structural approach actually investigates the structural stability of a community model, as opposed to the dynamical stability, which is the usual focus of coexistence theory. The underlying idea of the structural approach is very similar to the structural stability (1.2.2), with the advantage that the region of structural stability can be computed explicitly given the simple community model.

1.3 Current challenges of modern coexistence theory

As mentioned above, MCT tries to understand a community model in terms of their stabilizing and equalizing mechanisms. These have been introduced by Chesson (2000), which is considered as the founding paper of MCT. However, there are two sub-branches of MCT, one where stabilizing mechanisms are based on environmental fluctuations (the defining papers are Chesson (1994, 2003); Barabás *et al.* (2018); Ellner *et al.* (2019)) and one where stabilizing mechanisms are based on resource or other limiting factors partitioning (the defining papers are Chesson (1990); Adler *et al.* (2007); Carroll *et al.* (2011)). In both cases, equalizing mechanisms cannot ensure coexistence, in the absence of stabilizing mechanisms. They can only increase time to competitive exclusion.

Recently, Song *et al.* (2019) have shown that these two sub-branches of MCT are distinct through identifying different stabilizing and equalizing mechanisms. Additionally, they question the usefulness of stabilizing and equalizing mechanisms, as no mechanism was found to be purely stabilizing or equalizing (see also chapter 3). To clearly distinguish the two branches, I will use storage effect and relative non-linearity to talk about the first branch and niche and fitness differences to talk about the second branch. Note, however, that the literature also uses niche and fitness differences to talk about the first branch (e.g. Chesson (2000); Barabás *et al.* (2018)). Also, the different branches can be applied to the same underlying data, as done in Song *et al.* (2019) and Figure

2.1.

1.3.1 Analytical mathematics

The key concepts of MCT, storage effect and relative non-linearity on the one side and niche and fitness differences on the other, are based on analytical mathematics. As such, they can only be applied in communities that can be solved with analytical mathematics.

The storage effect and relative non-linearities are based on a second order Taylor approximation of the community model (Chesson, 2003). Quantifying storage effect and relative non-linearities in a new community model therefore requires extensive mathematics. For example Angert *et al.* (2009) contains a 17-page appendix and Zepeda & Martorell (2019) a 9-page appendix to compute the necessary variables. Similarly, the definition of niche and fitness differences were based on analytical mathematics and are therefore limited to simple communities (Chesson, 1990). This is most likely the largest burden of MCT, which limited its application to simple communities.

Recent theoretical advancements in MCT generalised both the notion of storage effect and relative non-linearity (Ellner *et al.*, 2016, 2019) and niche and fitness differences (Chapter 2), these generalisations do not depend on analytical mathematics. Letten *et al.* (2018) have already applied this method empirically. For comparison, the first empirical application of the analytical method came only 15 years after its definition (Chesson, 1994; Angert *et al.*, 2009).

1.3.2 Challenges for storage effect and relative non-linearity

Storage effect and relative non-linearity decompose the invasion growth rates of a species. As such, they are defined and useful for any community in which invasion growth rates correctly predict coexistence and inherit all challenges from invasion growth rates (see 1.2.3). They are therefore, in theory, applicable to a wide range of communities. Yet, empirical applications are scarce (Ellner *et al.*, 2019), due to its analytical complexity.

To decompose the invasion growth rates into relative non-linearity and storage effect, the growth rate of the invading species is compared to the scaled growth rates of the resident species. However, these scaling factors d_i are not uniquely defined if the species compete for more than one limiting resource (Barabás *et al.*, 2018; Ellner *et al.*, 2019). Altering the scaling factors will affect which mechanism we interpret as essential for coexistence. For example, Ellner *et al.* (2019) asserted that, by employing one set of scaling factors, facilitation is essential for coexistence, and then while employing a different set of scaling factors, facilitation had a negligible effect. Importantly, both interpretations are correct with respect to the proper scaling factors.

1.3.3 Challenges for niche and fitness differences

In short, most challenges of niche and fitness differences are related to communities with some less analytical tractability. Communities can be complex in many different ways, most notably species interactions can be complex, species interactions can be diverse, species types (e.g. producers, consumers, predators) can be diverse and coexistence conditions can be complicated. Unfortunately, most of MCT deals with communities that are none of the above (Adler *et al.*, 2007; Letten *et al.*, 2017; Narwani *et al.*, 2013; Levine & HilleRisLambers, 2009), let alone all of the above combined (but see Chu & Adler (2015)).

There are eleven different definitions of niche and fitness differences, which all have their different limitations and advantages. I will focus my list of challenges to the most applied definitions, i.e. Chesson (2013); Godoy & Levine (2014); Carroll *et al.* (2011). These are all based on the original definition of Chesson (1990).

Non-linear interactions

Communities with non-linear species interactions have been analysed with niche and fitness differences (Godoy & Levine, 2014; Letten *et al.*, 2017). However, to compute niche and fitness differences the community models were approximated by LV models, essentially ignoring non-linear or higher-order interactions. The definition of Carroll *et al.* (2011) may be applied to communities with non-linear interactions, however, as I show in chapter 3, this does not correctly interpret key assumptions of niche and fitness differences. That is, niche and fitness differences are essentially undefined for non-linear interactions.

Non-competitive species interactions

The original definition is only defined if $\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}} > 0$, otherwise the square root of negative numbers would lead to imaginary niche differences. α_{ii} and α_{jj} must be positive values, otherwise growth rates in monoculture are unbounded. Consequently, $\alpha_{ij}\alpha_{ji}$ must be positive too, which is the case if both are negative (mutualism) or both are positive (competition). Mutualism, while theoretically possible, has never been investigated with this definition of niche and fitness differences.

One-sided facilitation or predation are not defined by this definition and are consequently excluded from niche and fitness differences research (Chu & Adler, 2015; Narwani *et al.*, 2013). Bimler *et al.* (2018) redefined niche and fitness differences for communities with facilitation, however, their definition does not contain information about coexistence. Because niche and fitness differences are essentially only defined for competitive two-species communities, other trophic levels were excluded from the analysis.

Multi-species communities

The original definitions for niche and fitness differences are defined for two-species communities by comparing relative sensitivity α_{ij}/α_{jj} of the two-species ($\mathcal{N}_i = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$). This comparison, however, is bound to two-species communities and does not naturally extend to multispecies communities.

Carroll *et al.* (2011) and Carmel *et al.* (2017) have both attempted to extend the two-species comparisons to multispecies communities, essentially by taking community averages of the relative sensitivities α_{ij}/α_{jj}. While this gives expressions for multispecies niche and fitness differences, these cannot be interpreted in the light of coexistence. Two communities with identical values of niche and fitness differences may lead to coexistence once but not in the other community.

Limited collaborations

In short, niche and fitness differences are only defined for competitive two-species communities with linear species interactions. As a consequence, collaborations with other ecological fields are limited, as these often investigate more complex communities. For example, biodiversity-ecosystem function research often assumes that niche differences are responsible for the positive effect of species or trait richness on ecosystem function (Striebel *et al.*, 2009; Tilman *et al.*, 2014). However, this assumption has only rarely been verified with a proper definition of niche differences (Carroll *et al.*, 2011; Godoy *et al.*, 2020).

Multi-trophic communities

Niche and fitness differences were originally mediated via resource competition, but it has been recognised early that these could also be mediated via predators or mutualists (Chesson & Kuang, 2008; Petry *et al.*, 2018; Johnson & Bronstein, 2019). As MCT focuses on competing two-species communities these higher trophic levels have been excluded from the coexistence considerations. The higher trophic levels in both Chesson & Kuang (2008) and Johnson & Bronstein (2019) contain a self-regulating factor to avoid the extinction of these species.

However, as Godoy *et al.* (2018) point out, MCT should start to focus on the entire community, instead of just a competing sub-community. Again, this is not possible with the current definition of niche and fitness differences, as it would include both multi-species and non-competitive interactions.

1.4 Thesis outline

In this last section of the introduction I will lay out how the rest of my PhD thesis is structured. As a reminder, I chose thematic structure over a chronological order.

The key achievement of my PhD thesis is the reinterpretation of niche and fitness differences (Chapter 2). My reinterpretation is an independent approach to define niche and fitness differences, but interestingly, it reproduces earlier results on this topic (Chesson, 1990). This reinterpretation does not alter how we assess coexistence, rather it relies on invasion growth rates. My definition of niche and fitness differences does not improve our ability to assess the outcome of species interactions, but it improves our ability to interpret the outcome of species interactions.

In chapter 3, I compare this new approach with the traditional approach to measure niche and fitness differences. Specifically, I investigate the effect of higher order and non-linear interactions on niche and fitness differences, their effect on the outcome of species interactions and how we interpret their coexistence. Most importantly, I show that the omission of higher order interactions, when computing niche and fitness differences, leads to qualitatively wrong predictions concerning whether and why species coexist.

The reinterpretation of niche and fitness differences opens the door to analyse more complex communities. Multispecies communities were so far outside of the reach of MCT. In chapter 4, I show that species richness increases fitness differences, but not niche differences. This is an important step from simple two-species communities towards the higher complexity of natural communities.

MCT and biodiversity ecosystem function are closely related, as they both use niche differences to explain their results. Nonetheless, there are very few collaborations between the two fields. In chapter 5, I investigate the effects of trait richness on coexistence, niche and fitness differences, and ecosystem

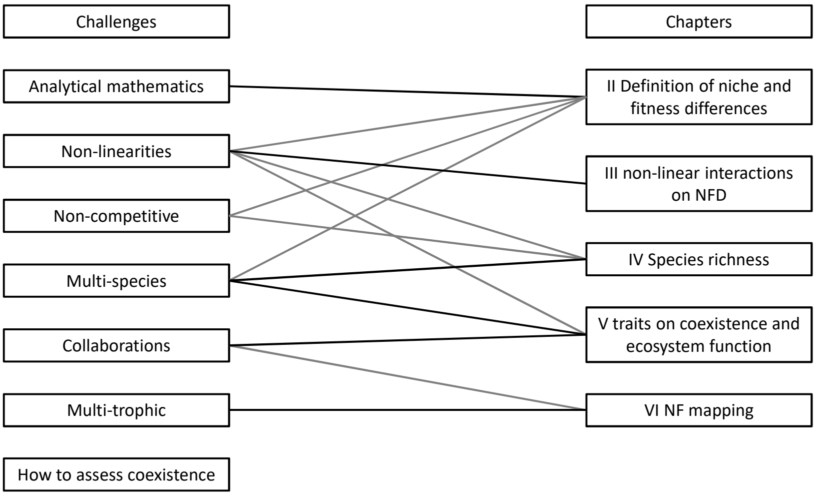

Figure 1.2: The various chapters of my PhD tackle different challenges of MCT. Many chapters tackle multiple challenges at the same time, but focus on one single challenge (black line). The only challenge that I did not address during my PhD was ”How to assess coexistence”.

function to close the gap between coexistence theory and biodiversity ecosystem functioning.

In chapter 6, I extend the focus of MCT towards the entire community. Most importantly, to communities with facilitative species interactions or species that depend on the presence of other species . I show how three higher-level processes can explain species coexistence in many different communities, regardless of the underlying community structure. I also show that MCT has so far only focused on a very limited range of these higher-level processes.

Finally, in my last chapter, I compare the results from different chapters to synthesize my work and discuss how recent advancements in MCT relate to its current challenges.

Chapter 2

Intuitive and broadly applicable definitions of niche and fitness differences

2.1 Abstract

Explaining nature's biodiversity is a key challenge for science. To persist, populations must be able to grow faster when rare, a feature called negative frequency dependence and quantified as 'niche differences' ($\mathcal{N}$) in modern coexistence theory. Here, we first show that available definitions of $\mathcal{N}$ differ in how $\mathcal{N}$ link to species interactions, are difficult to interpret, and often apply to specific community types only. We then present a new definition of $\mathcal{N}$ that is intuitive and applicable to a broader set of (modelled and empirical) communities than is currently the case, filling a main gap in the literature. Given $\mathcal{N}$, we also re-define fitness differences ($\mathcal{F}$) and illustrate how $\mathcal{N}$ and $\mathcal{F}$ determine coexistence. Finally, we demonstrate how to apply our definitions to theoretical models and experimental data, and provide ideas on how they can facilitate comparison and synthesis in community ecology.

2.2 Introduction

In order to persist through time, species must exhibit frequency dependent population growth. Natural communities host a multitude of mechanisms that can lead to frequency dependence. Well-known examples include resource partitioning (Adler *et al.*, 2007; Levine & HilleRisLambers, 2009), differential vulnerability to predators (Chesson & Kuang, 2008; Allan *et al.*, 2010; Carson &

Root, 2000), differential associations with mutualists (Siefert *et al.*, 2018; Johnson & Bronstein, 2019), phenological separation (Usinowicz *et al.*, 2017), or occupation of distinct microhabitats (Silvertown, 2004). These mechanisms have been collectively coined as stabilizing mechanisms that increase 'niche differences' (Chesson, 2000; Letten *et al.*, 2017; HilleRisLambers *et al.*, 2012).

In modern coexistence theory, one way of quantifying the strength of niche differences is to compare observed population growth with the population growth that is expected when niche differences would be absent (Chesson, 2000, 2003; Adler *et al.*, 2007, 2010). Without niche differences, one of the species will eventually exclude all others, where the rate of exclusion depends on the competitive advantage of the winner. This competitive advantage is often called 'fitness difference' (Chesson, 2000, 2003; Barabás *et al.*, 2018; Hart *et al.*, 2018). A key question is if niche differences in natural systems are sufficiently strong to overcome fitness differences and save species from extinction (Adler *et al.*, 2018b; Angert *et al.*, 2009; Usinowicz *et al.*, 2017; Hubbell, 2001; Connolly *et al.*, 2017; Harris *et al.*, 2017; Narwani *et al.*, 2013).

Niche and fitness differences formalise species persistence in a way that is phenomenological. That is, one does not need to specify the details of the community or its environment, but rather focuses on higher-level processes, i.e. how species grow under different circumstances. This feature would in principle allow synthetic studies across different community types and environmental conditions, with niche and fitness differences acting as common currency that represent the net outcome of detailed ecological mechanisms. Such studies are important because they foster a unified understanding of community composition (Adler *et al.*, 2018b) and facilitate studying how environmental context and community characteristics jointly influence species persistence, which can help understanding global change effects (Grainger *et al.*, 2019a).

At present, however, the application of niche and fitness differences is hampered by a lack of consensus on their mathematical definition. Indeed, the operationalisation of these concepts has been discussed for almost a century and new methods are being constantly proposed (Renkonen, 1938; Morisita, 1959; Hurlbert, 1978; Chesson, 1990, 2000, 2003; Carroll *et al.*, 2011; Bimler *et al.*, 2018), leading to a proliferation of mathematical definitions of niche and fitness differences. We identified 10 definitions available in the literature (Appendix A.1) and found that every single existing definition displays a number of features that limit its applicability. For instance, most of the definitions only apply to communities whose dynamics obey a specific mathematical model (Chesson, 1990; Adler *et al.*, 2007; Chesson & Kuang, 2008; Godoy & Levine, 2014; Bimler *et al.*, 2018; Saavedra *et al.*, 2017). This means that the applicability of these definitions is limited to specific community types. In addition, several definitions cannot be computed for communities with positive species interactions and/or more than two species. Also, not all definitions allow inference of coexistence or exclusion, i.e. niche and fitness differences do not predict whether species will persist or not (Apendix A). Finally, different definitions imply different ranges for niche and fitness differences. Hence, we cannot readily compare results from different authors (Grainger *et al.*, 2019a; Godoy & Levine, 2014; Chu & Adler, 2015; Song *et al.*, 2019) (Appendix A.1).

Here, we first show that available definitions of niche differences do not align with biological intuition and present a new definition that does. We also derive the corresponding definition of fitness differences and coexistence conditions. An important feature of these new definitions is that they apply to any mathematical model or empirical system driven by any mechanism, with the sole critical requirement that invasion analysis correctly predicts coexistence. The flexibility of the new definitions allows comparing different community types, containing an arbitrary number of species and a variety of species interactions, addressing a key limitation in theoretical ecology. Finally, we illustrate theoretical and experimental applications of the new definitions. To this end, we apply the definitions to various models representing a suite of interaction types. We also show how simple growth experiments suffice to quantify niche and fitness differences, using an empirical dataset of two picocyanobacteria competing for light.

2.3 Theory

2.3.1 A diversity of definitions

To facilitate interpretation and broad application, the definitions for niche and fitness differences should align with biological intuition. Intuition dictates that niche differentiation facilitates persistence ($\mathcal{N}$ increases as species persist more easily). In addition, a definition of $\mathcal{N}$ that is consistent with intuition must satisfy five constraints. First, when intra- and interspecific interactions are of equal size ($\alpha = -1$ in Fig. 2.1), individuals of both species are interchangeable: the effect an individual has on another individual does not depend on species identity. Thus, $\mathcal{N}$ should equal 0 (black triangle in Fig. 2.1) (Chesson, 1990). Second, when interspecific interactions are absent ($\alpha = 0$ in Fig. 2.1), each species grows as if other species are absent. Thus, $\mathcal{N}$ should be some predefined non-zero real number that indicates complete niche differentiation, e.g. 1 (black dot in Fig. 2.1) (Godoy & Levine, 2014). The third point is the logical consequence of these first two points: intermediate interspecific interaction strengths should result in $\mathcal{N}$ between 0 and 1 (solid rectangle in

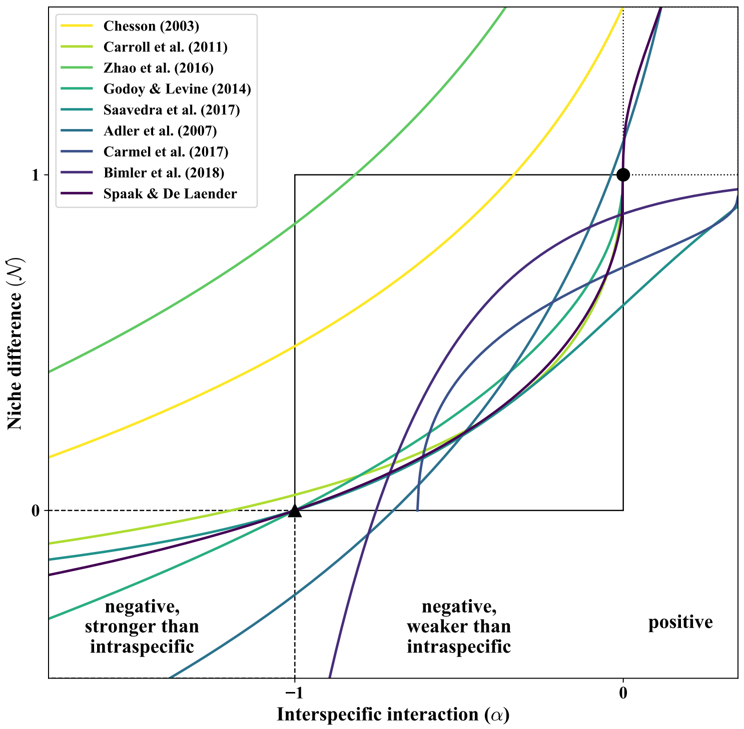

Figure 2.1: The modelled response of niche differences ($\mathcal{N}$) to the interspecific interaction strength α between two annual plants differs among available definitions. The black triangle indicates where inter- and intraspecific interactions are equal ($\alpha = -1$), and so species occupy the same niche, meaning that $\mathcal{N}$ should be 0. Communities with stronger interspecific interactions must have $\mathcal{N} < 0$ (dashed rectangle). The black dot indicates where species do not interact ($\alpha = 0$), and so species have completely different niches, meaning $\mathcal{N}$ should be 1. Consequently, communities in which interspecific interactions are positive ($\alpha > 0$) should have $\mathcal{N}$ larger than 1 (dotted rectangle). Finally, for all communities where $-1 \leq \alpha \leq 0$, $\mathcal{N}$ must have intermediate values ($0 \leq \mathcal{N} \leq 1$, solid rectangle). The new definition proposed here (red), which is applicable to a wide variety of models and experimental data (i.e. not only the annual plant model), complies with this biological intuition. Parameter values, a plot for the corresponding fitness differences ($\mathcal{F}$), and mathematical expressions of the $\mathcal{N}$ and $\mathcal{F}$ definitions are in appendix A.1.

Fig. 2.1). Fourth, when interspecific interactions are more negative than intraspecific interactions, persistence is 'harder' ($\mathcal{N}$ should be smaller) than if species occupied exactly the same niche ($\mathcal{N} = 0$). Consequently, $\mathcal{N}$ should be negative (dashed rectangle in Fig. 2.1), as has been stated before (Ke & Letten, 2018; Mordecai, 2011). Fifth, when interspecific interactions are positive, e.g. because of facilitation, the presence of other species makes persistence 'easier' ($\mathcal{N}$ should be greater) than if these other species would have no effect on the focal species (i.e. interspecific interactions are absent, in which case $\mathcal{N} = 1$). Thus, $\mathcal{N}$ should inevitably be greater than 1 (dotted rectangle in Fig. 2.1) when species interactions are positive.

We found that available definitions of $\mathcal{N}$ are unlikely to fulfil the five requirements outlined here. To show this, we computed $\mathcal{N}$ for the annual plant model, a workhorse of theoretical ecology (Adler *et al.*, 2007; Angert *et al.*, 2009; Levine & HilleRisLambers, 2009; Adler *et al.*, 2010, 2012; Godoy *et al.*, 2014; Germain *et al.*, 2016) (Fig. 2.1), using eight of the ten definitions for niche and fitness differences. The two other definitions cannot be applied to the annual plant model. All definitions return greater $\mathcal{N}$ as species interactions shift from strongly negative, over weakly negative, to positive. However, different definitions for niche difference imply a variety of niche difference responses to the strength and sign of species interactions (Fig. 2.1). In addition, these definitions do not map these species interactions to the intuitive niche difference values, as stated above (but see Chesson (1990); Godoy & Levine (2014); Chesson & Kuang (2008)). We therefore introduce, in the next section, a new definition that does align with biological intuition.

2.3.2 Defining niche differences based on biological intuition

Here, we first construct a general definition for $\mathcal{N}$ that fulfils the five requirements outlined in the previous section, and is therefore based on biological intuition. To construct a definition of $\mathcal{N}$, we start by considering the per capita growth of a species i

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, N_j) \tag{2.1}$$

where N_i, N_j are densities of species i and species j ($i \neq j$) with which i interacts. f_i can be essentially any function that describes the per-capita growth rate of species i. A discrete system $N_i(t+1) = N_i(t) f_i(N_i(t), N_j(t))$ can be analysed as well, by taking the natural logarithm i.e. $f_i'(N_i, N_j) = \log(f_i(N_i(t), N_j(t)))$ (Chesson, 1994, 2003). As done mostly in modern coexistence theory (but see Schreiber *et al.* (2019)), we do not consider Allee effects (positive density dependence), such that we can assume $f_i(0,0) > f_i(N_i,0)$: a species grows faster when its density is lower. While accounting for Allee effects is technically possible with the definitions proposed here, interpretation of $\mathcal{N}$ will be challenging (see below). Furthermore, we assume that each species has a stable monoculture equilibrium denoted N_i^* and that the invasion growth rate $f_i(0,N_j^*)$correctly predicts coexistence. That is, the two species i and j coexist if and only if both species have a positive 'invasion growth rate' ($f_i(0,N_j^*) > 0$). The invasion growth rate is the growth rate of a species when it is reduced to low density (≈ 0) and the other species is at its monoculture equilibrium density. Examples where invasion analysis does not predict coexistence are found in Barabás *et al.* (2018) and Schreiber *et al.* (2019). We only assume a fixed point equilibrium for notational simplicity, but the definitions also apply to a stationary distribution equilibrium.

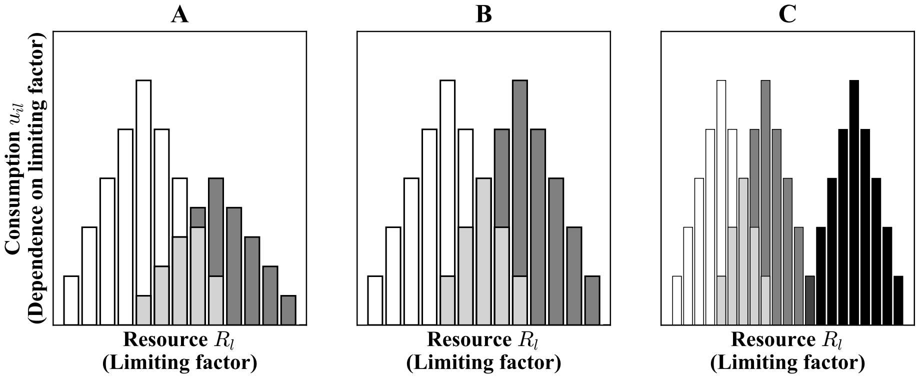

Figure 2.2: Species-specific influences on limiting factors (here, resources) for a two (A, B) and a three (C) species community. In the two-species community (A) the two species do not have the same total influence on the limiting factors, therefore the amount of shared resources is different ($1-\mathcal{N}_i = \frac{\text{light grey area}}{\text{white area}} \neq \frac{\text{light grey area}}{\text{grey area}} = 1-\mathcal{N}_j$). The conversion factors $c_i = \frac{\text{white area}}{\text{grey area}}$ are chosen such that the two species have the same total effect on limiting factors (B). Then, the two species also share an equal proportion of their resources. This is, however, not the case in a multispecies community (C) (Adler *et al.*, 2007), where the amount of shared resources is smaller for the black species than for the white species, even though all species consume the same total amount of resources. We therefore expect $\mathcal{N}_{black} \neq \mathcal{N}_{white}$.

Box 2.1: $\mathcal{N}$ and $\mathcal{F}$ for the MacArthur and Lotka-Volterra model

Consider a community of two species whose dynamics follow (MacArthur, 1970)

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_{l=1}^{m} u_{il} R_l - m_i \tag{2.2}$$

$$\frac{1}{R_l}\frac{dR_l}{dt} = K_l - R_l - \sum_{i=1}^{2} u_{il} N_i \tag{2.3}$$

Where u_{il} is the rate at which species i consumes resource l, R_l is the density of resource l, m_i is the loss rate and K_l is the resource's carrying capacity. We assume that the resource dynamics are faster than the dynamics of the consumers, such that R_l is always at equilibrium. In that case, the model simplifies to (MacArthur, 1970):

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_{l=1}^{m} u_{il} K_l - m_i - \sum_{l=1}^{m} u_{il} u_{jl} N_j - \sum_{l=1}^{m} u_{il}^2 N_i \tag{2.4}$$

Solving equations 2.21 and 2.22 yields (appendix A.3)

$$c_j = \sqrt{\frac{\sum_{l=1}^{m} u_{jl}^2}{\sum_{l=1}^{m} u_{il}^2}} \tag{2.5}$$

Thus, c indeed captures the species' total influence on limiting factors. Replacing the c's into the growth rates, one obtains (appendix A.4):

$$N_j^* = \frac{\sum_{l=1}^{m} u_{jl} K_l - m_j}{\sum_{l=1}^{m} u_{jl}^2} \tag{2.6}$$

$$f_i(0,0) = \sum_{l=1}^{m} u_{il} K_l - m_i \tag{2.7}$$

$$f_i(0,N_j^*) = \sum_{l=1}^{m} u_{il} K_l - m_i - \sum_{l=1}^{m} u_{il} u_{jl} \frac{\sum_{l=1}^{m} u_{jl} K_l - m_j}{\sum_{l=1}^{m} u_{jl}^2} \tag{2.8}$$

$$f_i(c_j N_j^*,0) = \sum_{l=1}^{m} u_{il} K_l - m_i - \sqrt{\frac{\sum_{l=1}^{m} u_{il}^2}{\sum_{l=1}^{m} u_{jl}^2}} \left(\sum_{l=1}^{m} u_{jl} K_l - m_j \right) \tag{2.9}$$

Finally, replacing these into eqs. 2.16 and 2.17, one obtains (appendix A.4):

$$\mathcal{N}_i = 1 - \frac{\sum_{l=1}^m u_{il}u_{jl}}{\sqrt{\sum_{l=1}^m u_{il}^2 \sum_{l=1}^m u_{jl}^2}} \tag{2.10}$$

$$\mathcal{F}_i = 1 - \frac{\sum_{l=1}^m u_{jl}K_l - m_j}{\sum_{l=1}^m u_{il}K_l - m_i}\sqrt{\frac{\sum_{l=1}^m u_{il}^2}{\sum_{l=1}^m u_{jl}^2}} \tag{2.11}$$

We now note that eq. 2.4 is equivalent to the Lotka-Volterra model ($\frac{1}{N_i}\frac{dN_i}{dt} = \mu_i - \alpha_{ii}N_i - \alpha_{ij}N_j$), where $\mu_i = \sum_{l=1}^m u_{il}K_l - m_i$, $\alpha_{ii} = \sum_{l=1}^m u_{il}^2$, and $\alpha_{ij} = \sum_{l=1}^m u_{il}u_{jl}$ are the intrinsic growth rate, the intraspecific interaction strength, and interspecific interaction strength, respectively. Plugging these expressions in eqs. 2.16 and 2.17 recovers equations for $\mathcal{N}$ and $\mathcal{F}$ that are equivalent to earlier versions of $\mathcal{N}$ and $\mathcal{F}$ in the Lotka-Volterra model (Chesson, 1990, 2000, 2013):

$$\mathcal{N}_i = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} \tag{2.12}$$

$$\mathcal{F}_i = 1 - \frac{\mu_j}{\mu_i}\sqrt{\frac{a_{ji}a_{ii}}{a_{jj}a_{ij}}} \tag{2.13}$$

When $\mathcal{N} = 0$, inter- and intraspecific interactions are equal. Thus, the identity of the individual does not matter, such that, in eq. 2.1, $f_i(N_i, N_j)$ is equivalent to writing $f_i(N_i + N_j, 0)$. However, one cannot simply sum species densities. For example, a large tree and a small forb may draw down the same resource. However, they will most likely do so to a different extent. Resource consumption of each individual tree may be much greater than the resource consumption of each individual forb. Therefore, we introduce a conversion factor, c_j, that translates the density of a species into a density of the other species, that would consume the same amount of resources. No mechanistic understanding of the species interactions is necessary to compute c_j, and as we show below, it can be estimated empirically. While the ecological interpretation of c is discussed below (Applications), we already stress that these are *not* the scaling factors known from modern coexistence theory (Chesson, 1994; Barabás *et al.*, 2018; Ellner *et al.*, 2019).

Hence, the growth of species i can be written as:

$$\mathcal{N} = 0 \Rightarrow f_i(N_i, N_j) = f_i(N_i + c_jN_j, 0) \tag{2.14}$$

When $\mathcal{N} = 1$, interspecific species interactions are absent. Thus, species j

has no effect on species i, and so species i grows as if species j were absent, i.e. we can put the density of j to zero:

$$\mathcal{N} = 1 \Rightarrow f_i(N_i, N_j) = f_i(N_i, 0) \tag{2.15}$$

Equations 2.1-2.15 hold for all densities N_i, N_j. However, we will now apply it to obtain species i's invasion growth rate, which allows interference about coexistence. This corresponds to choosing $N_i \approx 0$ and $N_j = N_j^*$, which is j's monoculture equilibrium. In this scenario, eqs. 2.14 and 2.15 become $\mathcal{N} = 0 \Rightarrow f_i(0, N_j^*) = f_i(c_j N_j^*, 0)$ and $\mathcal{N} = 1 \Rightarrow f_i(0, N_j^*) = f_i(0,0)$. Here, $f_i(0,0)$ is the intrinsic growth rate and $f_i(0, N_j^*)$is the invasion growth rate. For $f_i(c_j N_j^*, 0)$, we introduce the term no-niche growth rate of species i. This is the growth rate of species i if there was no niche differentiation, i.e. if $\mathcal{N}$ would be 0. Technically, the no-niche growth rate of species i is the growth rate at the converted monoculture density of its competitor (species j).

The main idea behind the new definitions is to let $\mathcal{N}$ fulfil the requirements from the previous section. The simplest way to do so is by writing $\mathcal{N}$ as a linear function that equates to 2.14 and 2.15 at the desired growth rates:

$$\mathcal{N}_i = \frac{f_i(0, N_j^*) - f_i(c_j N_j^*, 0)}{f_i(0,0) - f_i(c_j N_j^*, 0)} \tag{2.16}$$

This new definition by design fulfils the requirements, which can be seen when applying it to the annual plant model(Fig. 2.1). When species interact negatively and do so more within than between species, $\mathcal{N}_i$ is bounded in $[0,1]$ (solid rectangle). When interspecific interactions are more negative than intraspecific interactions, species grow slower when rare ($f_i(0, N_j^*) < f_i(c_j N_j^*, 0)$) and $\mathcal{N}_i$ will be negative (dashed rectangle). When interspecific effects are positive ($f_i(0,0) < f_i(0, N_j^*)$) $\mathcal{N}_i$ is larger than 1 (dotted rectangle).

This new definition should be interpreted as follows. The numerator of $\mathcal{N}_i$ compares the growth of species i when only interspecific interactions are present ($f_i(0, N_j^*)$) with its growth when only intraspecific interactions matter ($f_i(c_j N_j^*, 0)$). Note that in this last growth rate, $c_j N_j^*$ denotes a density of species i. Both growth rates are evaluated at the same total converted density, but at different frequencies of species i, being 0% in $f_i(0, N_j^*)$and 100% in $f_i(c_j N_j^*, 0)$. The numerator of $\mathcal{N}_i$ therefore effectively measures frequency dependence of species i (Adler *et al.*, 2007; Levine & HilleRisLambers, 2009). The denominator of $\mathcal{N}_i$, which is always positive and thus does not influence the sign of $\mathcal{N}_i$, compares the growth of species i when its density is ≈ 0 with its growth when its density is at the converted equilibrium density of j ($c_j N_j^*$).

Thus, the denominator of $\mathcal{N}_i$ measures the strength of species i's density dependence. $\mathcal{N}_i$ therefore measures the strength of frequency dependence, relative to that of density dependence. According to this new definition, and unlike almost all other definitions (but see Adler *et al.* (2007)), $\mathcal{N}_i$ is species-specific and is therefore not a community characteristic. However, $\mathcal{N}_i$ does depend on species j as well, as species j will influence species i's invasion and no-niche growth rates (eq. 2.16). In what follows, we use the subscript i ($\mathcal{N}_i$) only to distinguish between the niche differences of the species, and use $\mathcal{N}$ to refer to niche differences in general.

2.3.3 Fitness differences and coexistence

The novel definition of $\mathcal{N}$ implies a new definition of the fitness difference $\mathcal{F}$. Verbally, $\mathcal{F}$ should represent the per-capita growth rate when both species occupy the same niche, i.e. when $\mathcal{N} = 0$ (Adler *et al.*, 2010; Barabás *et al.*, 2018). Therefore

$$\mathcal{F}_i = \frac{f_i(c_j N_j^*, 0)}{f_i(0,0)} \tag{2.17}$$

$\mathcal{F}_i$ ranges from $-\infty$ to 1 (because we assume no Allee effects, i.e. $f_i(c_j N_j^*, 0) < f_i(0,0)$) and measures how well species i grows in the absence of frequency dependence (no-niche growth rate, numerator) (Adler *et al.*, 2007, 2010), compared to its intrinsic growth rate (denominator). When $\mathcal{F}_i$ is 0, species i is equally competitive as species j. Otherwise exactly one species, the competitive dominant, has $\mathcal{F}_i > 0$.

$\mathcal{N}$ and $\mathcal{F}$ both depend on the intrinsic and the no-niche growth rate. The no-niche growth rate itself depends implicitly on the invasion growth rate as well (see below eq. 2.21). In general, changing any underlying parameter will affect both $\mathcal{N}$ and $\mathcal{F}$, i.e. they are interdependent (Song *et al.*, 2019).

Now that we have defined both $\mathcal{N}$ and $\mathcal{F}$, we can evaluate when species i can coexist with species j. Interestingly, normalising the invasion growth rate by the intrinsic growth rate yields $\frac{f_i(0,N_j^*)}{f_i(0,0)} = \mathcal{N}_i + \mathcal{F}_i - \mathcal{N}_i \cdot \mathcal{F}_i$ (appendix A.2 Thus, i can persist within the community when[1]:

$$-\mathcal{F}_i < \frac{\mathcal{N}_i}{1 - \mathcal{N}_i} \tag{2.18}$$

---

[1] Assuming that $\mathcal{N}_i < 1$

This inequality formalizes the idea that species persist, when $\mathcal{N}$ "overcome" $\mathcal{F}$. However, the inequality is only meaningful if invasion growth rate correctly predicts coexistence. This inequality yields a number of important insights. First, as for $\mathcal{N}$, also $\mathcal{F}$ is species-specific. Taken together, this shows that the above inequality should therefore be considered as the condition for species i to persist. Only if all species from a community fulfil this inequality, all species will coexist. Second, the minus sign on the left hand side of eq. 2.18 shows that a high $\mathcal{F}_i$ implies a competitive advantage for species i, which is consistent with previous insights (Chesson, 2000, 2003; Adler *et al.*, 2007). Third, completely different niches are sufficient to overcome arbitrarily large $\mathcal{F}_i$ (i.e. $\mathcal{N} = 1 \Rightarrow -\mathcal{F} < \frac{1}{1-1} = \infty$). Conversely, if species occupy the same niche (i.e. $\mathcal{N} = 0 \Rightarrow -\mathcal{F} < \frac{0}{1-0} = 0$), coexistence is only possible under neutrality (i.e. $\mathcal{F}_i = \mathcal{F}_j = 0$). Fourth, species with negative $\mathcal{N}$ cannot coexist, as species' growth is positively frequency dependent: species grow faster when abundant (Mordecai, 2011; Ke & Letten, 2018; Schreiber *et al.*, 2019).

2.3.4 Extension beyond species pairs

The definitions for $\mathcal{N}$ and $\mathcal{F}$ naturally extend to communities composed of more than two species, hereafter 'multispecies communities'. To show this, we generalised the invasion growth rate and the no-niche growth rate to the case of multispecies communities (for technical details see appendix A.2):

$$\mathcal{N}_i = \frac{f_i(0, \boldsymbol{N}^{-i,*}) - f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0})}{f_i(0, \mathbf{0}) - f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0})} \tag{2.19}$$

$$\mathcal{F}_i = \frac{f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0})}{f_i(0, \mathbf{0})} \tag{2.20}$$

Here $\boldsymbol{N}^{-i,*}$ is the vector of equilibrium densities in the absence of species i, $\mathbf{0}$ denotes the absence of all species other than i, and similar to the definition for species pairs (eq. 2.16), c_{ij} converts densities of species j into i. These definitions measure the net effect of species interactions on $\mathcal{N}$ and $\mathcal{F}$, i.e. including direct, indirect (Godoy *et al.*, 2017) and higher order effects (Grilli *et al.*, 2017). More specifically, the interpretations given for the two-species community still apply, i.e. a species can persist if $-\mathcal{F}_i < \frac{\mathcal{N}_i}{1-\mathcal{N}_i}$ and the multispecies case fulfils the five constraints outlined above (appendix A.2). These interpretations are valid when (i) invasion analysis is possible and (ii) correctly predicts coexistence (Turelli, 1978; Chesson, 1994, 2000). In multispecies communities, but in some two-species communities as well, (i) and (ii) will sometimes not be met (Saavedra *et al.*, 2017; Barabás *et al.*, 2018).

2.4 Applications

2.4.1 Application to community models

The new definitions of $\mathcal{N}$ and $\mathcal{F}$ are applicable across various community types, driven by a variety of species interactions. To demonstrate this, we apply the definitions to five classic community types, and examine how the various growth rates and resulting c_i, c_j, $\mathcal{N}$ and $\mathcal{F}$ change between these types. Application to an empirical community, where species interactions may or may not be known a priori, is illustrated in the next section.

A first step in applying eqs. 2.16 and 2.17 to a model is the quantification of the factors c_i and c_j. The c convert species i to j and vice-versa, and so logically $c_j \cdot c_i = 1$. For example, if one tree influences resource levels ten times more than a forb ($c_{tree} = 10$), the forb influences resource levels ten times less than the tree ($c_{forb} = 1/10$). After conversion, both species thus have the same total influence on the environment. In Fig. 2.2A, we provide an example of two species consuming common resources. We converted their consumption rates such that total consumption is the same for both species (Fig. 2.2B): the white and the grey area are equal. This example highlights two results. First, the c, by equating the total influence on limiting factors, are needed to correctly compute niche differences. That is, they remove any effect fitness differences may have on niche overlap. Second, after conversion (Fig. 2.2B), both species now also happen to have the same proportion of shared limiting factors ($1 - \mathcal{N}_i =$ light grey region $= 1 - \mathcal{N}_j$). We can therefore find c by solving the equations

$$1 - \mathcal{N}_i = 1 - \mathcal{N}_j \tag{2.21}$$

$$c_i \cdot c_j = 1 \tag{2.22}$$

In Box 1, we illustrate this first step, and the calculation of $\mathcal{N}$ and $\mathcal{F}$, for a MacArthur consumer-resource model. We then convert this model into the well-known Lotka-Volterra model to express $\mathcal{N}$ and $\mathcal{F}$ using interaction coefficients. This exercise highlight the following results. First, while $\mathcal{N}$ and $\mathcal{F}$ are species-specific, they can be identical between species in species pairs competing for shared resources. Indeed, changing i for j in eq. 2.10 shows that $\mathcal{N}_i = \mathcal{N}_j$. However, they cease to be identical when including more than two

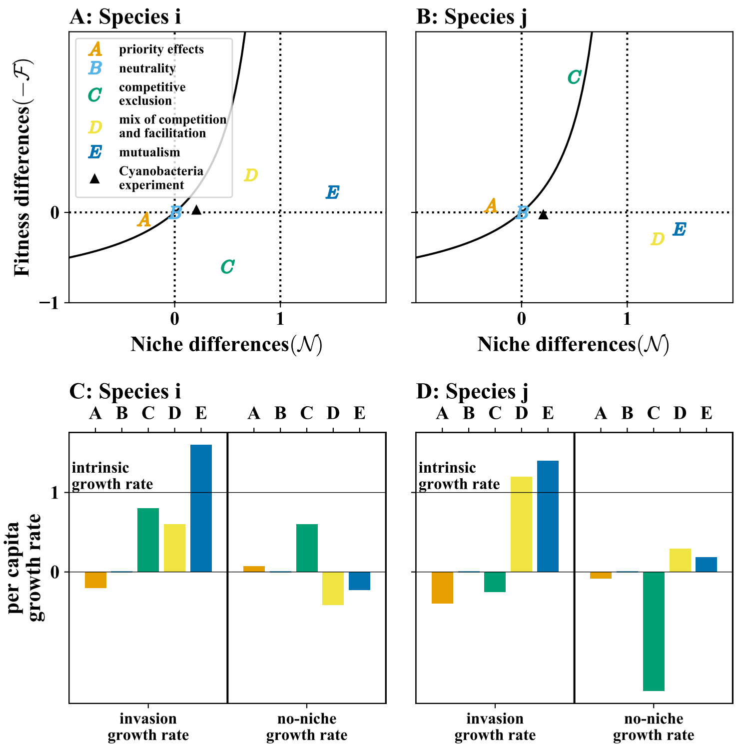

Figure 2.3: $\mathcal{N}$ and $\mathcal{F}$ applied to common two-species communities. Panels A and B show the distribution of $\mathcal{N}$ and $\mathcal{F}$ for species i and species j respectively, where color codes refer to different communities (see legend). A-E are communities simulated with Lotka-Volterra models, while 'experiment' refers to the performed experiment (Fig. 2.4). Only species in the grey area have a positive invasion growth rate, i.e. only those persist (Barabás *et al.*, 2018; Chesson, 2000). Panels C and D compares the invasion and the no-niche growth rate to the intrinsic growth rate (=1; vertical full line).

species, as can be seen from Fig. 2.2C. Indeed, niche overlap, and therefore $\mathcal{N}$, is species-specific in that case. Second, the new definitions of $\mathcal{N}$ and $\mathcal{F}$, when applied to the Lotka-Volterra model, collapse to equivalent definitions for $\mathcal{N}$ and $\mathcal{F}$ previously found for the same model (Chesson, 1990). This shows that these new definitions, which apply to any model (for which invasion analysis is possible and useful) still agree with the definitions found for this particular model. Third, c_i carries a biological interpretation: in the MacArthur model, c_i indeed increases with the total influence on limiting factors (see eq. 2.5). This shows why the conversion factors c_i differs completely from the scaling factors used in modern coexistence theory: the latter are weights used to partition invasion growth rates (Chesson, 1994; Barabás *et al.*, 2018; Ellner *et al.*, 2019) (appendix A.3).

This last feature is independent of the specific model formulation, i.e. it extends beyond the McArthur resource model to any model in which two species interact through resource consumption, resource consumption stimulates growth, and species consume more of a resource when its availability is higher. In appendix A.4, we show a mathematical proof that in such a model, increasing the resource consumption of species i will increase c_i, i.e. c is linked to the total resource consumption of a species. Finding the c when species have positive effects on each other (for example by generating resources or by limiting the efficacy of a predator) requires additional considerations, which are discussed in appendix A.2 and A.4.

Finally, we apply equations 2.16 and 2.17 to examine how the various growth rates underlying $\mathcal{N}$ and $\mathcal{F}$, as well as $\mathcal{N}$ and $\mathcal{F}$ itself, change across community types (Fig. 2.3) modelled using Lotka-Volterra equations (Appendix A.4). Priority effects occur when interspecific interactions are stronger than intraspecific interactions, i.e. $(f_i(0, N_j^*) < f_i(c_j N_j^*)$, Fig. 2.3 C,D). Neutrality occurs when $\mathcal{N} = \mathcal{F} = 0$ (Adler *et al.*, 2007). Competitive exclusion represents the well-known case where $\mathcal{N}$ are not large enough to compensate for $\mathcal{F}$: only the competitive dominant (species i) persists (Ke & Letten, 2018; Chesson, 2013).

For the case of "mix of competition and facilitation" (Zarnetske *et al.*, 2013; Adler *et al.*, 2018b)) and mutualism, one or both species have an invasion growth rate that is higher than their intrinsic growth rate: these species profit from other species and thus grow better together than alone. Therefore, these species have $\mathcal{N} > 1$. In these cases, $\mathcal{F}$ matter less for persistence (they only indicate the winner when $\mathcal{N} = 0$).

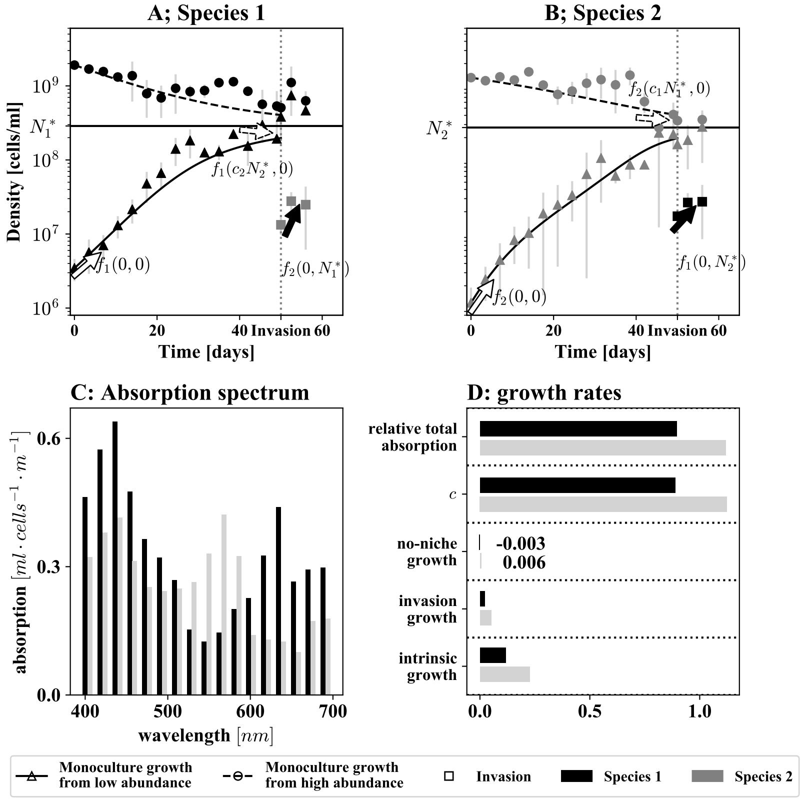

Figure 2.4: $\mathcal{N}$ and $\mathcal{F}$ applied to experimental data for two marine cyanobacteria species from the genus *Synechococcus*, sampled in the Baltic sea (Stomp *et al.*, 2004). A and B: Population growth in the different experiments with different starting conditions. Fitted lines are obtained by interpolating growth rates. Importantly, to compute $\mathcal{N}$ and $\mathcal{F}$ one does not have to fit a community model through the measured densities. The arrows indicate the growth rates we measured to quantify $\mathcal{N}$ and $\mathcal{F}$. Error bars (grey) show one standard deviation (3 replicates). C: The two species have different absorption spectra and therefore partition light usage. A spectrum of the incoming light intensity can be found in Appendix A.5. D: The experiment confirms that the species compete and coexist, as the invasion growth rate is positive, but smaller than the intrinsic growth rate. The conversion factor c is very similar to the relative total absorption of the two species, confirming its interpretation as a measure of total influence on the limiting factors (see eq. 2.5). An automated code to compute $\mathcal{N}$ and $\mathcal{F}$ from such experimental data can be found on https://github.com/juergspaak/NFD_definitions.

2.4.2 Application to experiments

The applicability of the new $\mathcal{N}$ and $\mathcal{F}$ definitions extends beyond models and can be used to analyse coexistence empirically. In these experiments, one needs to measure the various growth rates from equations 2.16 and 2.17 to quantify $\mathcal{N}$ and $\mathcal{F}$ (Fig. 2.4). These experiments also allow estimating the factors c_i and c_j, giving insight in the species' total influence on limiting factors. Importantly, the definitions can be computed directly from the measured growth rates, without any assumption on the species' ecology or the need to fit a model, contrary to many other definitions. This is particularly useful since natural communities are typically governed by a multitude of species interactions, many of which will be unknown (Montoya *et al.*, 2006; Carrara *et al.*, 2015).

To illustrate the application to experimental data, we performed an experiment in which we measured growth of two picocyanobacteria species competing for light (Fig. 2.4). Detailed experimental methods can be found in the appendix A.5. The two picocyanobacteria species contain different pigments (phycocyanobilin and phycoerithrobilin), which allow them to absorb different wavelengths of light (Fig. 2.4 C) Six *et al.* (2007). Because light colour usages of these two species partly overlap, exactly as did resource usage in the MacArthur model (Fig. 2.2), we expected that $0 < \mathcal{N} < 1$ (i.e. species compete). Experiments and field data have shown that pigmentation differences among picocyanobacteria lead to a resource (light) partitioning that is sufficiently strong to allow coexistence (Stomp *et al.*, 2004, 2007a,b). We therefore also expected that $-\mathcal{F} < \frac{\mathcal{N}}{1-\mathcal{N}}$ (i.e. coexistence).

Three growth curves per species suffice to quantify $\mathcal{N}$ and $\mathcal{F}$ for a two-species community (Fig. 2.4). First (Fig. 2.4A and B, triangles), we grew both species in a monoculture, starting from low density to obtain the intrinsic growth rate. Second (Fig. 2.4A and B, circles), we grew both species in a monoculture starting from a density higher than their equilibrium density to obtain the no-niche growth rate. The growth rate at which the density of the focal species reaches that of the converted equilibrium density of its competitor ($c_jN_j^*$), is the no-niche growth rate. In this particular case, the no-niche growth rates proved very small because $N_i^* \approx c_jN_j^*$ and $N_j^* \approx c_iN_i^*$. An example where this is not the case can be found in figure 2.5. Third (Fig. 2.4A and B, squares), we introduced each of both species into a monoculture at equilibrium of its competitor to obtain the invasion growth rates. More precisely, we introduced 5% of the invading species' equilibrium density (Gallego *et al.*, 2019; Narwani *et al.*, 2013). We estimated all these growth rates as $f_i(N_i(t),0) \approx \log\left(\frac{N_i(t+\Delta t)}{N_i(t)}\right)/\Delta t$ with $\Delta t = 84$ hours. We then fitted a univariate spline to estimate these growth rates at the various densities. Finally, we were able to use the measured growth rates to solve the equation 2.21 and thus obtain c_i and c_j, as well as $\mathcal{N}$ and $\mathcal{F}$. Importantly, the converted equilibrium density at which the no-niche growth rate is measured is part of the solution to these equations.

The results of the experiment confirmed our expectations: species compete for light ($0 < \mathcal{N} < 1$ for both species) and coexist (see triangle in Fig. 2.3). The estimated growth rates show that both species can grow independently of each other (positive intrinsic growth rate), and can invade each other's monoculture (positive invasion growth rate). Their no-niche growth rate is much smaller than their corresponding intrinsic growth rates, and slightly negative for species 1 but positive for species 2. This shows that removing all niche differentiation would lead to the exclusion of species 1, as is also seen from these species' fitness differences $\mathcal{F}$ (Fig. 2.3). Finally, we found the conversion factors c_i and c_j to match the relative total resource consumption (absorption) of the two species (figure 2.4 D). This finding aligns with the theoretical result that the conversion factors link to the total influence on limiting factors (available resources) and confirms that these species compete for light. While this experimental procedure is applied to fast growing communities, this design can be applied to communities with slow growing species as well. Any method that allows estimating per-capita growth is sufficient, but obviously these methods will vary with the considered community. For annual plants, for example, one may sow different quantities of seeds, ranging from low to above equilibrium density, in plots, and measure their growth.

2.5 Discussion

In this chapter, we propose new definitions for $\mathcal{N}$ and $\mathcal{F}$ that are biologically intuitive by design. The approach is similar to Carroll *et al.* (2011) in that it allows computing $\mathcal{N}$ and $\mathcal{F}$ from simulations or experimental data, without the knowledge of the underlying mechanisms. When applied to the Lotka-Volterra model for competing species, the definitions collapse to equivalent mathematical expressions of $\mathcal{N}$ and $\mathcal{F}$ found before (Chesson, 1990, 2013), while still being applicable to a large body of community models. This indicates that there is potential for these new definitions to unify existing definitions (Chesson, 2000; Godoy & Levine, 2014; Barabás *et al.*, 2018; Carroll *et al.*, 2011), while enforcing the connection between theory and biological intuition (HilleRisLambers *et al.*, 2012; Adler *et al.*, 2007, 2010).

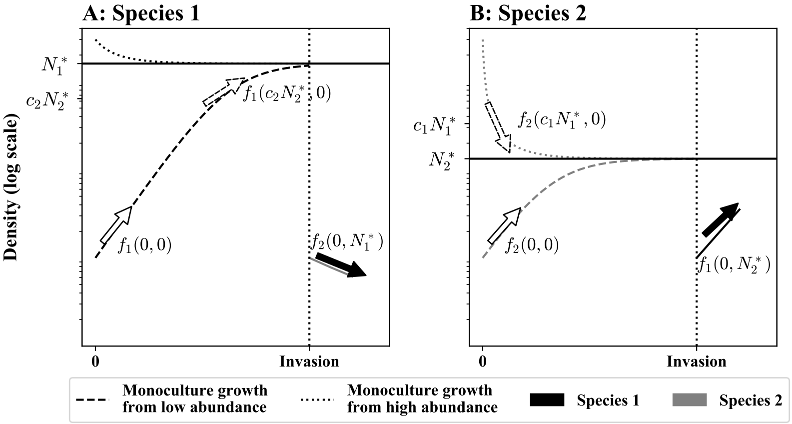

Figure 2.5: $\mathcal{N}$ and $\mathcal{F}$ applied to simulated experimental data using case C from figure 2.3, where $c_1N_1^*$ ($c_2N_2^*$) and N_2^* (N_1^*) differ substantially, unlike in Figure 2.4. For the competitive inferior (species 2), we have $c_1N_1^* > N_2^*$, while for the other species (species 1) we have, $c_2N_2^* < N_1^*$. For species 1 the second experiment (dotted black line) proved not necessary to compute $\mathcal{N}$ and $\mathcal{F}$, as the no-niche growth rate can be estimated from experiment one (dashed arrow, dashed black line). However, in general one will not know in advance for which species experiment two is unnecessary.

2.5.1 Specificities and limitations

$\mathcal{N}$ and $\mathcal{F}$, as defined in this chapter, differ from other definitions of niche and fitness differences. Most notably, the proposed definitions are not based on specific mathematical models, apply to communities with positive species interactions and/or more than two species, and allow inference of coexistence or exclusion. Thus, the new definitions notably extend modern coexistence theory based on invasion analyses. The structural approach of Saavedra *et al.* (2017) is the only definition for niche and fitness differences which can analyse communities that are outside of the scope of this new definition, as it does not depend on invasion analysis. They define $\mathcal{N}$ and $\mathcal{F}$ for a community in which the equilibrium point of the community can be described as $\boldsymbol{r} = \boldsymbol{\alpha} \boldsymbol{N}^*$, where $\boldsymbol{\alpha}$ is a n by n matrix containing the species interactions and $\boldsymbol{r}$ is a vector containing the intrinsic growth rates (or equivalent), which may be subject to additional constraints (Song *et al.*, 2018). Finally, there are still communities that are beyond the reach of all definitions for $\mathcal{N}$ and $\mathcal{F}$, including the newly proposed definitions: multispecies communities with non-linear interspecific species interactions (therefore excluding the approach of Saavedra *et al.* (2017), but see (Cenci & Saavedra, 2018)), and not allowing invasion analysis (therefore excluding the approaches of Chesson (2003); Carmel *et al.* (2017); Carroll *et al.* (2011) and the definitions proposed here).

The reliance on invasion analysis is a first limitation of the proposed definitions, as it is for many other definitions (Carmel *et al.*, 2017; Carroll *et al.*, 2011; Zhao *et al.*, 2016; Chesson, 2003). This reliance means that one should be able to compute the invasion growth rate for each species and that the invasion growth rates correctly predict coexistence. This can limit the applicability of the definitions in two ways. First, there will be communities in which invasion analysis does not correctly predict coexistence (Barabás *et al.*, 2018). An example is the annual plant model combined with positive frequency dependency proposed by Schreiber *et al.* (2019). Second, invasion analysis requires that all species within each S-1 subcommunity (the community without the invading species) stably co-exist. A well-known counter example is the rock-paper-scissors community, in which the whole community can coexist, while each two-species subcommunity is not stable (Grilli *et al.*, 2017). While these two assumptions will be met for most two-species communities, we expect they will be increasingly violated as communities contain more species (Saavedra *et al.*, 2017).

A second limitation of the new definitions is the difficulty of interpretation that arises in communities with Allee effects. The proof that the c_i have a unique solution demands Allee effects to be absent (Appendix A.2). Consequently, Allee effects imply that species may have multiple $\mathcal{N}$ and $\mathcal{F}$. This highlights the meaning of Allee effects: species change their dependence on limiting factors with their density. While the new definitions do allow computing these multiple $\mathcal{N}$ and $\mathcal{F}$, it is at present not clear how to interpret them.

2.5.2 The need for new definitions

With already ten definitions at hand, one may ask why we need new definitions for niche and fitness differences. We identify at least two reasons. A first reason deals with the complexity of many community models. Many approaches to compute niche and fitness differences first fit a community model to empirical data and then perform maths to link the model to $\mathcal{N}$ and $\mathcal{F}$ (Chesson, 1990; Godoy & Levine, 2014; Bimler *et al.*, 2018; Saavedra *et al.*, 2017). One challenge is that these maths are often non-trivial (e.g. Saavedra *et al.* (2017); Godoy & Levine (2014); Carmel *et al.* (2017)) and one needs to resort into simplifying the community model (Godoy & Levine, 2014; Letten *et al.*, 2017). This may lead to the omission of mechanisms contributing to $\mathcal{N}$ (Chu & Adler, 2015). For example, niche partitioning could arise at different life stages of a species (Moll & Brown, 2008), or through its interactions with resources (Chesson, 1990), predators (Chesson & Kuang, 2008) or mutualists (Johnson & Bronstein, 2019) and will be affected by environmental change (Rey *et al.*, 2017; Wainwright *et al.*, 2019). An important advantage of the new definitions is that they do not require analytical solutions of a community model or even a community model at all: one can simply simulate or perform the experiments described in the section ”Application to experiments” and measure the resulting growth rates to compute $\mathcal{N}$ and $\mathcal{F}$. Thus, the model or experimental community can be used in its full complexity, capturing all mechanisms potentially contributing to $\mathcal{N}$ and $\mathcal{F}$.

A second reason is that the analysis of communities with non-competitive interactions (e.g. mutualistic and facilitative, Fig. 2.1) and multiple species (eq. 2.19) is urgently needed. Indeed, such communities have often been analysed in a suboptimal way. For example Narwani *et al.* (2017) tested whether closely related fresh water green algae are more likely to coexist due to higher niche differentiation. However, $\mathcal{N}$ could not be computed when species interactions were positive. Similarly, in a meta-analysis on terrestrial plants, Adler *et al.* (2018b) were not able to compute $\mathcal{N}$ for one third of the data, as they contained positive interactions. Chu & Adler (2015) measured $\mathcal{N}$ and $\mathcal{F}$ in an age structured model for perennial plants fitted to long-term demographic data, Petry *et al.* (2018) measured the effects of ant consumption on $\mathcal{N}$ and $\mathcal{F}$ and Veresoglou *et al.* (2018) reanalysed data from the ”BIODEPTH” grassland biodiversity experiment. While these studies do report computed $\mathcal{N}$ and $\mathcal{F}$ for multispecies communities, the interpretation of these variables is difficult, as they do not predict coexistence in multispecies communities.

2.5.3 New insights and outstanding questions

Historically, $\mathcal{N}$ measured the proportion of resources not shared by two species (Hurlbert, 1978). Being a proportion, $\mathcal{N}$ was bound between 0 and 1 (Godoy & Levine, 2014). Linking a mechanistic (resource uptake) model to the Lotka-Volterra model (MacArthur, 1970; Chesson, 1990) was a key step in exploring $\mathcal{N}$ beyond the traditional range $[0,1]$. Recent research interpreted negative $\mathcal{N}$ as a sign that interspecific interactions are stronger than intraspecific interactions, leading to priority effects (Ke & Letten, 2018). The interpretation that $\mathcal{N}$ greater than 1 imply positive interspecific interactions is a logical next step. Our results show that this interpretation is correct when both species have symmetric positive effects on each other, but also that species benefiting from other species (e.g. "mix of competition and facilitation" in Fig. 2.3) would have $\mathcal{N} > 1$.

The results suggest that $\mathcal{N}$ and $\mathcal{F}$ are species-specific properties. While this idea has already been introduced by Adler *et al.* (2007), virtually all other definitions consider $\mathcal{N}$ a community property. This likely stems from the fact that most definitions focus on two species communities with competitive interactions, in which case niche differences are the proportion of shared resources, which is the same for both species (Fig. 2.2 B, light grey area). Therefore, in this particular case, the two species have the same $\mathcal{N}$, leading to the impression that $\mathcal{N}$ is a community property.

The results spur three outstanding questions on species coexistence. A first question deals with the variable c, that we found increases with the total influence on limiting factors, both for a class of resource competition models and empirically. However, our mechanistic understanding of these factors is absent for models beyond the ones considered here, notably in systems not driven by resource competition. Most notably, we do not know how c relates to the presence of limiting factors with negative effects on per-capita growth. A second outstanding question deals with the location of species from complex communities on the $\mathcal{N}$ and $\mathcal{F}$ plane from Fig. 2.3. While these positions may be trivial in some two-species communities, they will not be in large complex networks with a high number of indirect effects, possibly leading to surprising conclusions regarding the contribution of stabilizing and equalizing forces to persistence. A third question deals with the extended applicability the new definitions offer to modern coexistence theory. This applicability would allow asking how $\mathcal{N}$ or $\mathcal{F}$ compare across community types, mechanisms, and environments. Thus, the new definitions enable cross-community comparisons in a way that at present is not possible. One could, for example, examine how species from different community types position in Fig.2.3, to ask if community types that are thought to harbour a more diverse set of mechanisms fostering coexistence (e.g. annual plants) distinguish from community types that appear to have little possibilities for niche differentiation (e.g. phytoplankton (Hutchinson, 1959)).

Within a community type (e.g. phytoplankton), one could compare the stabilizing effect of various mechanisms. For example, we found $\mathcal{N}$ and $\mathcal{F}$ to indicate coexistence in a classic example of a community driven by partitioning of the light spectrum through phenotypic differences (i.e. pigmentation, see Fig. 2.3) (Stomp *et al.*, 2004). How does the stabilizing strength of these phenotypic differences (driving $\mathcal{N}$) compare to the strength of other relevant mechanisms (e.g. competition for mineral nutrients, allelopathy)? One could also examine how environmental changes alter the sign of species interactions (Olsen *et al.*, 2016; Baert *et al.*, 2016; Song *et al.*, 2020b) impact the persistence, since the proposed definitions accommodate various interaction types.

In conclusion, our results offer a new perspective on two concepts that underpin biodiversity science, and foster their intuitive biological interpretation (Fig. 2.1). The developed theory is applicable to a variety of ecological communities, regardless of community complexity, and without the need of mathematical skills (Ellner *et al.*, 2019), for any system in which invasion analysis is possible and correctly determines coexistence. The fact that various communities can be analysed with one approach is a major step forward. Taken together, the novel definitions of $\mathcal{N}$ and $\mathcal{F}$ promote conceptual unification and facilitate empirical research in community ecology and biodiversity science.

2.5.4 Supplementary Information

An automated code that will compute $\mathcal{N}$ and $\mathcal{F}$ for any given ecological model or experimental data is available. The code is available in Python and in R on https://github.com/juergspaak/NFD_definitions.

2.6 Acknowledgments

We thank O.Godoy, G. Barabas and S. Ellner for comments on earlier versions of this manuscript. We thank J. Virgo for conducting the experiment. F.D.L. received support from grants of the University of Namur (FSR Impulsionnel 48454E1), and the Fund for Scientific Research, FNRS (PDR T.0048.16).

Chapter 3

The effect of non-linear competitive interactions on quantifying niche and fitness differences

3.1 Abstract

Niche and fitness differences of modern coexistence theory separate mechanism into stabilizing and equalizing. This decomposition can help us predict and understand coexistence, however, it may depend on the method to assess niche and fitness differences. We apply two different methods to assess niche and fitness differences to four well known community models. We show that the most often used method, which is based on linear approximations of the community model and does not capture the full community dynamics, can lead to wrong predictions of coexistence and leads to wrong interpretations of stabilizing and equalizing mechanisms. Conversely, a novel method to assess niche and fitness differences based on the full community model and intuition correctly identifies all stabilizing and equalizing mechanisms. Importantly, it reveals that essentially all mechanisms are both stabilizing and equalizing, even those thought to be purely stabilizing. We therefore propose to compare the predictions and explanations of multiple niche and fitness differences methods o broaden our understanding of coexistence.

3.2 Introduction

Explaining biodiversity is a prime objective of ecology (Hutchinson, 1959). There are many different approaches to address this objective. Neutral theory focuses on regional processes (Hubbell, 2001), stability analysis focuses on properties of the community matrix (Allesina & Tang, 2012), contemporary niche theory focuses on investigating species' limiting factors (Tilman, 1982), and modern coexistence theory focuses on separating niche and fitness differences that help and hamper coexistence (Chesson, 2000).

Niche and fitness differences are two central concepts in coexistence theory which help us to *predict* and *understand* species coexistence. Whether or not species coexist depends on how much species limit each other's growth compared to their own growth. From a mechanistic standpoint, various factors such as resources or predators, can limit population growth. Population sizes will on their turn influence these factors (Meszéna *et al.*, 2006) (e.g. by depleting resources or by boosting the population size of their predators), as such creating the regulating feedback underpinning growth limitation. Thus, mechanistically, niche differences measure how independent the feedback loop of two species are. If the feedback loops are completely independent, then niche differences are 1, conversely, if the feedback loops are equivalent niche differences are 0. Fitness differences measure the relative strength of the feedback loops. Species will coexist when niche differences ($\mathcal{N}$) overcome fitness differences ($\mathcal{F}$) (Adler *et al.*, 2007; Chesson, 2000).

Unfortunately, computing niche and fitness differences taking into account the full complexity of limiting factors is not a straightforward task. Most available methods therefore apply to simple models only (Spaak & De Laender, 2020), where the details of population regulation are omitted. These models write per capita population growth as linear functions of the competitor's densities, which then act as limiting factors, in lieu of the actual factors that underpin species interactions. Doing so is done by approximating the equations of the more complex models with linear functions around some predefined equilibrium point (Letten *et al.*, 2017; Ke & Letten, 2018; Godoy & Levine, 2014; Carroll *et al.*, 2011) , often making various assumptions on the time-scales at which the limiting factors vary, as well as on the persistence of these factors. While these simplifying assumptions will by design be violated in certain conditions, we do not know the implications of such violations for our capacity to predict and understand coexistence. Such knowledge is important for correct application of coexistence theory, as is choosing the appropriate definition of niche and fitness difference (Godwin *et al.*, 2020).

Here, we examine to what extent linear approximations of community models affect our ability to predict and understand coexistence. To this end, we assemble four community models, three of which explicitly model limiting factors, and one which considers direct non-linear effects of population density on per-capita growth. We approximate all four models with linear functions and compare how the resulting niche and fitness differences differ from those of the full models including limiting factors and direct non-linear interactions. Based on this comparison, we first develop criteria to test whether the approximated models affect our ability to predict and understand coexistence. Then, we graphically represent the assumptions made by the approximation method and show that these simplifications can have a large effect on the community dynamics. Importantly, we show, contrary to our expectation, that these simplifications reduce our ability to predict coexistence, it classified coexisting species as non-coexisting and vice-versa. Finally, we also show that linear approximation misses new features that expand our understanding of coexistence. For example, changes in mortality rate can affect niche differences, niche and fitness differences can depend non-monotonically on resource supply rates and changes in resource supply rates may alter competition from negative to positive frequency dependent.

3.3 Methods

Four community models have so far been approximated by linear, i.e. Lotka-Volterra, model to compute niche and fitness differences: Species competing for substitutional resources with a Holling type 1 response (Chesson, 1990) and a Holling type 2 response (Letten *et al.*, 2017), species competing for essential resources with a Holling type 2 response (Letten *et al.*, 2017) and the annual plant model (Godoy & Levine, 2014). We used the linear approximation of each of these models from the literature and computed niche and fitness differences ($\mathcal{N}^A$ and $\mathcal{F}^A$) with the corresponding definition (Chesson, 1990). The superscript A denotes the fact that these are based on the **a**pproximated models. To compute niche and fitness differences of the full model ($\mathcal{N}^C$ and $\mathcal{F}^C$) we use the method outlined in (Spaak & De Laender, 2020). The superscript C denotes the fact that these are based on the full (**c**omplex) models.

3.3.1 Niche and fitness differences based on approximated models

Linear approximation of a model consists of writing these models (given by $\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, N_j)$) in Lotka-Volterra model form:

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i\left(1 - \alpha_{ii}N_i - \alpha_{ij}N_j\right) \tag{3.1}$$

Where N_i is the density of species i, r_i is the intrinsic growth rate, α_{ii} and α_{ij} are the intra- and interspecific competition coefficients. This involves writing the

α_{ij} of equation 3.1 as a function of the model parameters. Generally speaking, the linear approximations are defined to match the zero net growth isoclines (ZNGI) , i.e. $f_i(N_i, N_j) = 0 \Leftrightarrow 1 - \alpha_{ii}N_i - \alpha_{ij}N_j = 0$. In principal this means: $\alpha_{ii} = 1/N_i^{C,*}$ and $\alpha_{ij} = \left(N_i^{C,*} - N_i^*\right) / \left(N_i^{C,*}N_j^*\right)$, where $N_i^{C,*}$ is the equilibrium density of species i in monoculture; N_i^* and N_j^* are the equilibrium densities of species i and j in the two-species community. Nonetheless, we show below, that the approximations do sometimes not correctly approximate the equilibrium densities, because they are not defined on the real $N_i^{C,*}$, but rather an approximation thereof. The r_i are equivalent to the intrinsic growth rates, i.e. $r_i = f_i(0,0)$. For all other values of N_i and N_j the linearisation is an increasingly crude approximation. Table 3.1 summarizes the linear approximation for all these models. Given the interaction coefficients α_{ij} we can compute $\mathcal{N}^A$ and $\mathcal{F}^A$ as (Chesson, 1990):

$$\mathcal{N}_i^A = 1 - \sqrt{\frac{\alpha_{ji}\alpha_{ij}}{\alpha_{ii}\alpha_{jj}}} \tag{3.2}$$

$$\mathcal{F}_i^A = 1 - \sqrt{\frac{\alpha_{ii}\alpha_{ij}}{\alpha_{ji}\alpha_{jj}}} \tag{3.3}$$

Note that we slightly change the definition of $\mathcal{F}_i^A$ by defining $\mathcal{F}_i^A = 1 - \sqrt{\frac{\alpha_{ii}\alpha_{ij}}{\alpha_{ji}\alpha_{jj}}}$ instead of the more usual $\mathcal{F}_i^A = \sqrt{\frac{\alpha_{ii}\alpha_{ij}}{\alpha_{ji}\alpha_{jj}}}$. This change is purely aesthetic to ensure consistency between $\mathcal{F}_i^A$ and $\mathcal{F}_i^C$, it does not affect the properties of $\mathcal{F}^A$.

3.3.2 Niche and fitness differences based on the full model

We computed $\mathcal{N}^C$ and $\mathcal{F}^C$ for the full model based on a recently developed method (Spaak & De Laender, 2020). Briefly, this method ensures that species with independent feedback loops have $\mathcal{N}^C = 1$, while species with equivalent feedback loops have $\mathcal{N}^C = 0$. Thus, the method critically depends on invasion analysis correctly predicting coexistence for the model it is applied to (Spaak & De Laender, 2020; Barabás *et al.*, 2018; Chesson, 1994; Pande *et al.*, 2019). The invasion growth rate of a species i is its growth rate when the resident species j is at its monoculture equilibrium density. More precisely, for a model given by the per-capita growth rate $\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, N_j)$ Spaak & De Laender (2020) define

$\mathcal{N}^C$ and $\mathcal{F}^C$ as

$$\mathcal{N}_i^C = \frac{f_i(0,N_j^*) - f_i(c_jN_j^{C,*},0)}{f_i(0,0) - f_i(c_jN_j^{C,*},0)} \tag{3.4}$$

$$\mathcal{F}_i^C = \frac{f_i(c_jN_j^{C,*},0)}{f_i(0,0)} \tag{3.5}$$

where $N_j^{C,*}$ is, as above, the monoculture equilibrium density of species j and c_j is a conversion factor that converts densities of species j to densities of species i, it ensures that both species have the same dependence on limiting factors. c_j is the solution of the equation $|1-\mathcal{N}_i^C| = |1-\mathcal{N}_j^C|$ (Appendix B.6)

Equation 3.4 compares the actual invasion growth rate of species i ($f_i(0,N_j^{C,*})$) to the hypothetical invasion growth rate when the two species had independent feedback loops ($f_i(0,0)$) and to another hypothetical invasion growth rate when the two species had identical feedback loops ($f_i(c_jN_j^{C,*},0)$).

3.3.3 Predicting and understanding coexistence

For $\mathcal{N}^A$ and $\mathcal{F}^A$ or to correctly predict coexistence they need to correctly predict the outcome of species interactions. For a two species community there are three such outcomes (Tilman, 1982).

First, priority effects where the outcome of competition depends on the starting conditions, this is only possible with positive frequency dependence, i.e. negative niche differences (Ke & Letten, 2018). Second, coexistence where both species persist indefinitely, this is only possible with negative frequency dependence, i.e. positive niche differences. Third, competitive exclusion, where the competitive dominant species excludes the other species. This can happen with both negative and positive niche differences, and depends on the fitness differences ($\frac{1-\mathcal{N}^C}{\mathcal{N}^C}\mathcal{F}^C < -1$). When $\mathcal{N}^C$ and $\mathcal{F}^C$ or $\mathcal{N}^A$ and $\mathcal{F}^A$ correctly predict these three outcomes for a given model, we consider these to correctly *predict* coexistence.

For $\mathcal{N}^A$ and $\mathcal{F}^A$ or $\mathcal{N}^C$ and $\mathcal{F}^C$ to correctly *understand* coexistence, they need to correctly reflect the mechanisms driving the outcome of species interactions. $\mathcal{N}$ measures the difference between the niches of two species. When the two species do not interact with each other, because they occupy completely different niches, then $\mathcal{N}$ should reflect total niche differences , i.e. $\mathcal{N} = 1$ (Spaak & De Laender, 2020). Conversely, if two species occupy the same niche, then $\mathcal{N}$ should be 0. Testing whether two species occupy the same niche is very difficult in general, as one may not know whether the species do differ

Name	Model	r_i	α_{ij}
Substit-resources Holling type 1	$\frac{1}{N_i} \cdot \frac{dN_i}{dt} = \sum_l w_{il} R_l - m_i$ $\frac{1}{R_l} \frac{dR_l}{dt} = S_l - R_l - \sum_j u_{lj} N_j$	$\sum_l w_{il} S_l - m_i$	$\frac{\sum_l w_{il} u_{lj}}{\sum_l w_{il} S_l - m_i}$
Substit-resources Holling type 2	$\frac{1}{N_i} \cdot \frac{dN_i}{dt} = \frac{\sum_l w_{il} R_l}{k_i + \sum_l w_{il} R_l} - m_i$ $\frac{dR_l}{dt} = S_l - R_l - \sum_j u_{lj} N_j$	$\frac{\sum_l w_{il} S_l}{k_i + \sum_l w_{il} S_l} - m_i$	$\frac{\sum_l w_{il} u_{lj}}{\sum_l w_{il} S_l - \frac{k_i m_i}{1 - m_i}}$
Essential-resources Holling type 2	$\frac{1}{N_i} \cdot \frac{dN_i}{dt} = \min_l \left(\frac{w_{il} R_l}{R_l + k_{il}} \right) - m_i$ $\frac{dR_l}{dt} = S_l - R_l - \sum_j u_{lj} N_j$	$\min_l \left(\frac{w_{il} S_l}{S_l + k_{il}} \right) - m_i$	$\frac{u_{L_i j}}{S_{L_i} - R^*_{iL_i}}$
Annual plant	$\frac{N_i(t+1)}{N_i(t)} = (1 - g_i)(1 - m_i) + \frac{g_i \lambda_i}{1 + \sum_j \alpha_{ij} g_j N_j(t)}$	$\frac{g_i \lambda_i}{1 - (1 - g_i)(1 - m_i)} - 1$	$\frac{g_j \alpha_{ij}}{r_i}$

Table 3.1: We consider four community models of which the full equations are given ('Model'), as well as their linear approximation as reported before (Chesson, 1990; Godoy *et al.*, 2014; Letten *et al.*, 2017). The linearized versions of these models are reconstructed by replacing r_i and α_{ij} in equation 3.1 by the expressions in the corresponding columns. The first three models are resource explicit models. For these models w_{il} is the conversion of resource to biomass, u_{li} is the utilisation of resource l by species i, m_i is the mortality rate, S_l is the resource supply and k_i respectively k_{il} are half-saturation constants. Consistently, subscripts i and l stand for species and resources, respectively. Subscript L_i is the index of the more limiting resource of species i in monoculture. In the annual plant model g_i is the germination rate, m_i is the mortality rate (traditionally the model uses the survival rate $s_i = 1 - m_i$), λ_i is the net-production rate and α_{ij} is the intra- or interspecific interaction.

Criteria	Substit-resources Holling type 1		Substit-resources Holling type 2		Essential-resources Holling type 2		Annual plant	
	$\mathcal{N}^C,\mathcal{F}^C$	$\mathcal{N}^A,\mathcal{F}^A$	$\mathcal{N}^C,\mathcal{F}^C$	$\mathcal{N}^A,\mathcal{F}^A$	$\mathcal{N}^C,\mathcal{F}^C$	$\mathcal{N}^A,\mathcal{F}^A$	$\mathcal{N}^C,\mathcal{F}^C$	$\mathcal{N}^A,\mathcal{F}^A$
Comp. exclustion	✓	X	✓	X	✓	X	✓	✓
Coex.	✓	X	✓	X	✓	✓	✓	✓
Priority effects	✓	X	✓	X	✓	X	✓	✓
Same niche	✓	X	✓	X	✓	X	=	=
No interaction	✓	✓	✓	✓	✓	✓	✓	✓
Stabilizing mechanism	✓	X	✓	X	✓	X	≠	≠

Table 3.2: How $\mathcal{N}^A$ and $\mathcal{F}^A$ or $\mathcal{N}^C$ and $\mathcal{F}^C$ *predict* (first three rows) and *understand* (last three rows) coexistence across the four investigated models (columns). ✓indicates correct prediction respectively explanation, X indicates wrong prediction or explanation A ✓in the column "Coex." indicates that the method correctly predicts coexistence for each community in which the species coexist. The same holds for the columns "Comp. exclusion" and "Priority effects". The annual plant model does not explicitly consider limiting factors, so there is no clear criteria for asserting that both species occupy the same niche, the two methods however agree perfectly, i.e. $\mathcal{N}^C = 0 \Leftrightarrow \mathcal{N}^A = 0$, which we indicate with a "=" (see Appendix B.5). Similarly, there is no clear criteria for asserting that a mechanism is stabilizing, and we found that the two definitions do not agree on this (indicated with "≠").

in any not-investigate niche axis. However, in the special cases where there is only one limiting factor, e.g. because species compete only for one resource, species must occupy the same niche.

In addition, to *understand* species coexistence,$\mathcal{N}^A$ and $\mathcal{F}^A$ or $\mathcal{N}^C$ and $\mathcal{F}^C$ need to correctly categorize changes in a model's parameter as stabilizing and/or equalizing mechanisms. That is, changes that affect niche differences are called stabilizing, while they are equalizing when they affect fitness differences. Importantly, mechanism can be both stabilizing and equalizing. We will call any mechanism that only affects niche or fitness differences purely stabilizing or equalizing, respectively.

3.4 Results

$\mathcal{N}^A$ and $\mathcal{F}^A$ can be considered linear approximations of the per-capita growth rates, i.e. $f_i(N_i, N_j) \approx r_i \cdot (1 - \sum_j \alpha_{ij} N_j)$. Through this approximation we often loose information about community dynamics, most notably higher order interactions (Grilli *et al.*, 2017; Levine *et al.*, 2017) or explicit interactions with limiting resources (Letten & Stouffer, 2019). Importantly, the linearisation does not account for substitutable resources to go extinct (Chesson, 1990; Letten *et al.*, 2017), or for the fact that the identity of the essential resource that is limiting to a species can change during competition, independent of changes in the resource supply point (Letten *et al.*, 2017). Extinction of a resource becomes more likely with an increasing number of resources and should therefore not be seen as a special case, but rather as the norm (Holt, 1977; Abrams, 1983, 1980; Letten & Stouffer, 2019). As expected, the linearisation gives a poor approximation of the growth rates in general, and of the invasion growth rate especially, for all four models (Fig. 3.1).

3.4.1 When approximations do not correctly predict coexistence

Table 3.2 summarizes how $\mathcal{N}^A$ and $\mathcal{F}^A$ or $\mathcal{N}^C$ and $\mathcal{F}^C$ predict coexistence. $\mathcal{N}^C$ and $\mathcal{F}^C$ correctly predict the outcome of competition, as long as invasion analysis correctly predicts the outcome of competition (Spaak & De Laender, 2020). This is the case for the investigated models if no resources go extinct (Letten *et al.*, 2017; Tilman, 1982; Adler *et al.*, 2007; Godoy *et al.*, 2014; MacArthur, 1970; Chesson, 1990). However, communities with more than two resources (only for the substitutable resource models) may have multiple possible outcomes of competition, depending on the starting densities (Appendix B.1). $\mathcal{N}^C$ and $\mathcal{F}^C$ correctly predicts one of these equilibria, the equilibrium that is attained when either of the two species starts as an invader.

$\mathcal{N}^A$ and $\mathcal{F}^A$ correctly predicted the outcome of interaction for the annual plant model and for the substitutable resource models, when no resources go extinct. However, in some other cases, $\mathcal{N}^A$ and $\mathcal{F}^A$ do not correctly predict the outcome of competition (Appendix B.1 and B.2).

3.4.2 Approximations limit understanding of coexistence

The approximations $\mathcal{N}^A$ and $\mathcal{F}^A$ do mostly not correctly explain coexistence, even when they correctly predict coexistence.

For all investigated models $\mathcal{N}^C$ and $\mathcal{F}^C$ correctly identify when two species occupy the same niche ($\mathcal{N} = 0$). Conversely, $\mathcal{N}^A$ and $\mathcal{F}^A$ do correctly identify

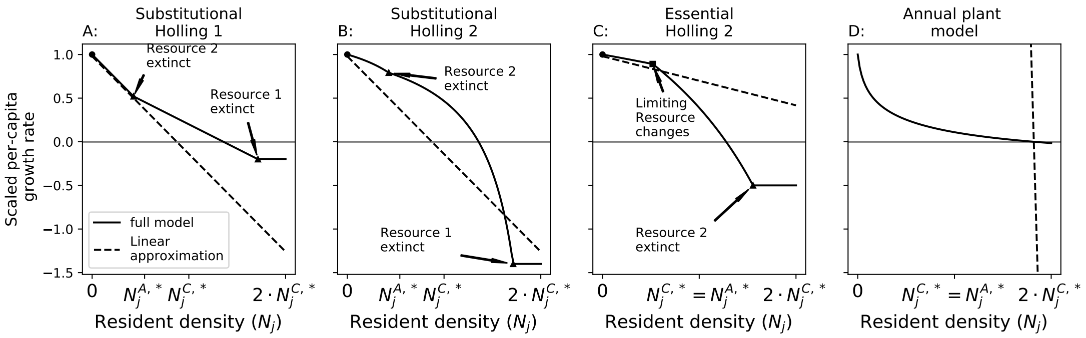

Figure 3.1: Scaled per capita growth rates of the focal species (y-axis) as a function of the resident species density (x-axis) for the four full models (solid line $= f_i(0, N_j)/f_i(0,0)$) and their linear approximations (dashed $= 1 - a_{ij}N_j$). The linear approximations do not capture the full complexity of the models and deviate substantially from the full model. Two main differences between the approximation and the full model stand out: First (A and B), the approximated equilibrium density of the resident $N_j^{A,*}$ is smaller than the exact resident's equilibrium density $N_j^{C,*}$ (indicated by different labels for $N_j^{A,*}$ and $N_j^{C,*}$). Second (A,B and C), the density for zero-net growth is not equal for the approximation and the full model (intersection with grey line). These two differences occur because the linearisation does not account for resources that go extinct (black triangles, A,B,C) or changes in which essential resource is limiting (black square, C). The full model eventually transforms into a horizontal like (A,B,C) when all resources are extinct and growth rates reduce to the density-independent mortality rates. These differences can lead to wrong predictions about the outcome of competition (see Table 3.2). Chosen parameters (A,B,C) are equivalent to Fig. 3.2.

this case in the annual plant model, but not in any of the resource-explicit community models. When one of the two resources goes extinct (for both species in monoculture, outside the dotted lines in figure 3.2, A,B,D,E), then the two species compete for only one resource and must have identical feedback loops. Consequently, the two species must have no niche differences. None the less, $\mathcal{N}^A \neq 0$ for these resource supply points. Similarly, for the competition for essential resources, the linearisation method predicts $\mathcal{N}^A = 0$ for a community with priority effects (Appendix B.2), which contradicts prior findings (Ke & Letten, 2018; Mordecai, 2011; Spaak & De Laender, 2020). Both the approximation and the full $\mathcal{N}$ and $\mathcal{F}$ give exactly the same predictions for the absence of niche difference in the annual plant model, i.e. $\mathcal{N}^C = 0 \Leftrightarrow \mathcal{N}^A = 0$, which we interpret as both methods correctly predict if the two species occupy the same niche. Both the approximation and the full niche and fitness differences correctly predict when the two species don't interact and must have $\mathcal{N} = 1$.

Any mechanism that is purely equalizing cannot alter the outcome of competition from coexistence to priority effects or vice versa (Ke & Letten, 2018). Therefore, any mechanism that alters the outcome of competition in that way must be stabilizing.

The approximations $\mathcal{N}^A$ and $\mathcal{F}^A$ do not correctly classify equalizing and stabilizing mechanisms. The approximation classifies any mechanism in the resource competition models that does not affect resource utilisation u_{li} or the conversion efficiency w_{il} as purely equalizing; Mechanisms that affect u_{li} or w_{il} are both equalizing and stabilizing. Importantly, it classifies changes in resource supply rate and changes in mortality to be purely equalizing. Yet we found that changes in mortality can alter the outcome of competition from priority effects to coexistence in certain conditions, and therefore must be stabilizing (Appendix B.1). $\mathcal{N}^C$ and $\mathcal{F}^C$ correctly predict that changes in mortality are stabilizing, as they affect $\mathcal{N}_i^C$ (Fig 3.3).

Changes in resource supply rates can be stabilizing mechanism as well. Given two species, the resource supply rates determine whether both species are limited by the same resources (and consequently must have $\mathcal{N} = 0$) or whether the species coexist (and consequently must have $\mathcal{N} > 0$). Therefore, changes in resource supply rates can be stabilizing mechanisms. In general, $\mathcal{N}^C$ and $\mathcal{F}^C$ predict that essentially all mechanisms are both stabilizing and equalizing (Song *et al.*, 2019).

$\mathcal{N}^C$ and $\mathcal{F}^C$ also highlight the existence of maxima and minima for $\mathcal{N}^C$ as a new insight. Importantly, the location of these local maxima and minima can be found geometrically, similar to the coexistence region (Appendix B.3). The existence of these maxima and minima is unexpected, but not counter-intuitive. We keep all community parameters fixed except S_1. For small values

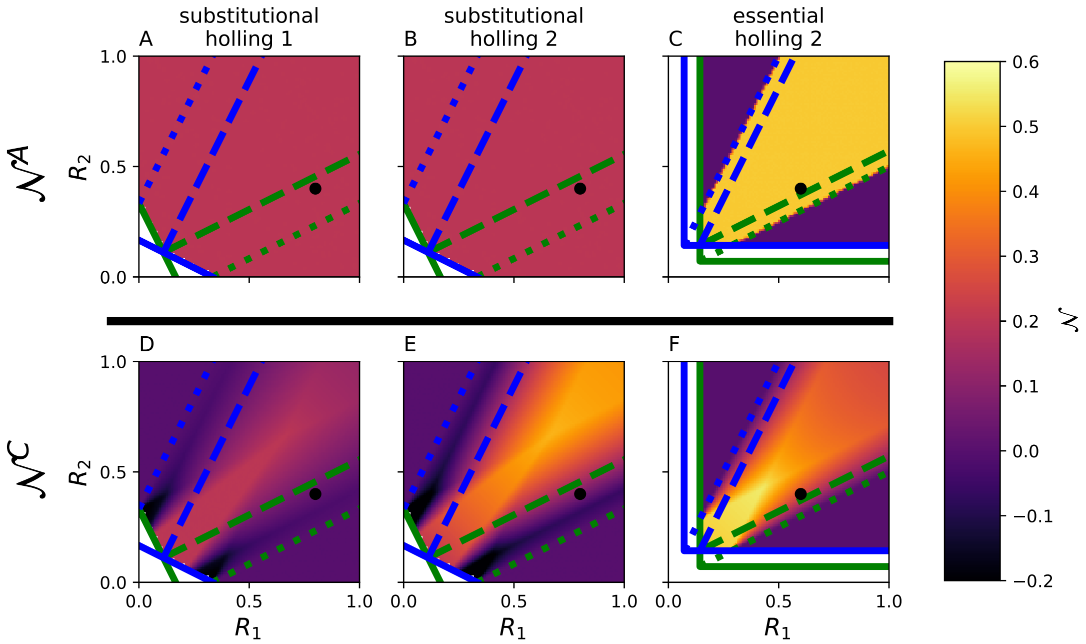

Figure 3.2: $\mathcal{N}$ (color) as a function of the resource supply point for the three different resource explicit community models. $\mathcal{N}^A$ and $\mathcal{N}^C$ are not defined when one species cannot survive in monoculture (white regions). A,B: $\mathcal{N}^A$ is independent of resource supply point for substitutable resources. Moreover, the functional response to resource concentrations does not affect $\mathcal{N}^A$ (given u_{li} and w_{il}). In the region where both species are limited by only one resource (above blue dotted and below green dotted line) $\mathcal{N}^A$ is non-zero, contrary to the assumption that species competing for one resource must have $\mathcal{N} = 0$. C: $\mathcal{N}^A$ is only affected by changes in the resource supply point if the limiting resource changes for a species (crossing a dotted line). This change from $\mathcal{N}^A \neq 0$ to $\mathcal{N}^A = 0$, however, is discontinuous. D,E,F: $\mathcal{N}^C$ continuously depends on changes in resource supply point and features local maxima (D-F) and minima (D,E). $\mathcal{N}^C$ correctly predicts $\mathcal{N}^C = 0$ in the region where both species are limited by the same resource. Green and blue solid lines are the ZNGI, dashed lines delimit the coexistence region and dotted lines delimit the region where both species are limited by the same resource. Black dot represents the resource supply point taken for Fig. 3.1 and 3.3.

of S_1 both species are limited by R_1 only, hence we must have $\mathcal{N} = 0$, for intermediate values of S_1 the species coexist, hence $\mathcal{N} > 0$, for large values of S_1 the species are limited by R_2, hence $\mathcal{N} = 0$. Consequently, $\mathcal{N}$ depends in a non-monotonic way on S_1 and will therefore exhibit a maximum. We should therefore expect that $\mathcal{N}$ depends in a non-monotonic way on simultaneous changes of both S_l, as it indeed does.

Importantly, the new findings, changes or mortality or resources supply point are stabilizing, are not based on the specificities of $\mathcal{N}^C$ and $\mathcal{F}^C$. Rather the argumentation is based on intuitive knowledge of niche differences only. It must therefore apply to any niche and fitness differences definition.

Another new insight from $\mathcal{N}^C$ and $\mathcal{F}^C$ is that competition for substitutable resources can lead to negative $\mathcal{N}_i^C$, i.e. positive frequency dependence, for certain resource supply point. However, even for these resource supply point, the community will not be driven by priority effects. This highlights that negative niche differences (and thus positive frequency dependence) are necessary but not sufficient conditions for priority effects. If fitness differences are to strong, one species will exclude the other, regardless of the initial condition, which is the case in this scenario (Ke & Letten, 2018). $\mathcal{N}^C$ and $\mathcal{F}^C$ do therefore not predict another outcome of competition than the resource competition theory by Tilman (1982). Positive frequency dependence arises when species consume more of the resource that limits their competitor most (Ke & Letten, 2018). For the resource supply point chosen in figure 3.2D the blue species drives resource 2 to extinction in monoculture. The red species, as an invader, will therefore only consume resource 1 and have a horizontal utilisation vector. The red species therefore consumes only the favoured resource of its competitor (blue species), which leads to positive frequency dependence (Ke & Letten, 2018). A condition for $\mathcal{N}^C < 0$ is therefore that resources go extinct, which is why $\mathcal{N}^C < 0$ does not occur for essential resources, as species in monoculture can't drive essential resources to extinction.

3.5 Discussion

The prevailing approach to compute niche and fitness differences is to simplify community models through linearisation (Godwin *et al.*, 2020; Godoy & Levine, 2014; Letten *et al.*, 2017; Chesson, 1990). We show that this approach results in niche and fitness differences that differ quantitatively and qualitatively from approaches taking into account non-linear species interactions. Including the non-linear species interactions improves our ability to predict and understand coexistence.

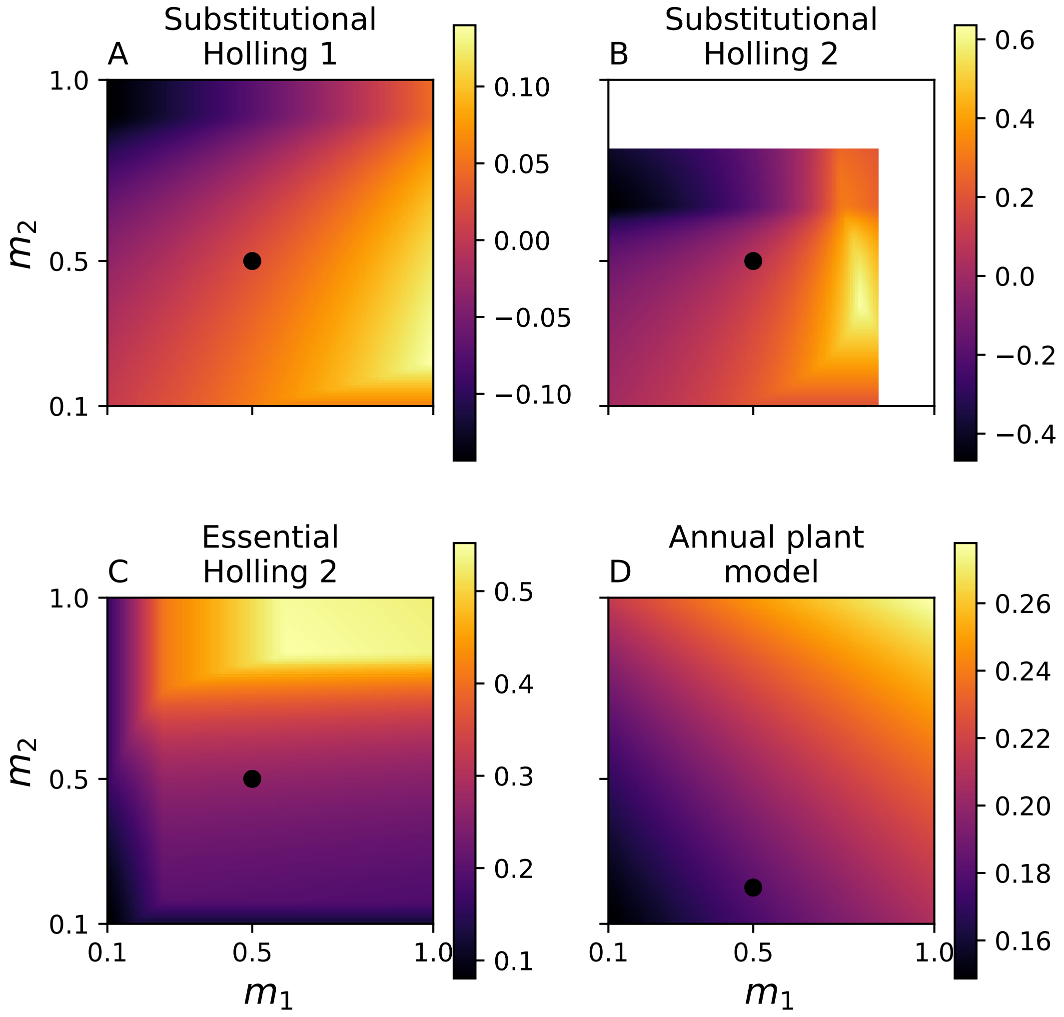

Figure 3.3: $\mathcal{N}^C$ (color) as a function of mortality for the four investigated models. Mortality has a non-monotonic effect on $\mathcal{N}^C$ and may lead to local maxima and minima of $\mathcal{N}^C$ (panel B), similar to changes in the resource supply point. Blank areas (Panel B) indicate too high mortality for species persistence. Parameters (except mortality) are chosen such as in fig. 3.1, the black dot represents the same mortality as in fig. 3.1.

3.5.1 We should not continue to use linear approximations to compute niche and fitness differences

We identified those cases for which $\mathcal{N}^A$ and $\mathcal{F}^A$ do and do not correctly predict coexistence. One might argue, that these are unprobable special cases or that a better linear approximation might correctly predict coexistence. For example, the method defined by Carroll *et al.* (2011) could be seen as another type of linear approximation, chosen such that the invasion and intrinsic growth rates are identical to those of the full community model. Other possible choices would be a Taylor expansion (Allesina & Tang, 2012) or a linear regression approach (Godwin *et al.*, 2020). Applying these alternative approximations can lead to different *predictions* of species coexistence than those presented here (Godwin *et al.*, 2020). However, none of them are likely to advance our *understanding* of coexistence, as they ignore important non-linear features of the community model (Appendix B.4).

Niche and fitness differences should facilitate understanding of species coexistence by disentangling stabilizing from equalizing mechanisms. We have shown that essentially all mechanisms are both stabilizing and equalizing, as they can alter the outcome of competition from priority effects to coexistence. Yet the linear approximation $\mathcal{N}^A$ and $\mathcal{F}^A$ predict that only very few mechanisms are stabilizing. Importantly, this is not only the case for some limited supply rates or other parameter ranges, but applies to essentially all mechanisms.

Finally, niche and fitness differences based on the linearisation approach are so far only defined for a two species community without facilitation (Bimler *et al.*, 2018; Carroll *et al.*, 2011). It is therefore not well suited to solve future problems in coexistence theory (Godoy *et al.*, 2018; Levine *et al.*, 2017; Serván *et al.*, 2018).

3.5.2 New insights

We analysed niche and fitness differences for four well-known community models, taking into account their full complexity without doing any approximations. This led to three new insights.

First, changes in mortality can affect both niche and fitness differences, contrary to earlier results (Chesson, 2000; Godoy *et al.*, 2014; Barabás *et al.*, 2018; Petry *et al.*, 2018; Letten *et al.*, 2017). This confirms the earlier findings from Song *et al.* (2019) who found that niche and fitness differences are interdependent. Except in some special cases, changing any parameter always affected both niche and fitness differences. We found no mechanism that acts solely equalizing or stabilizing.

Second, niche differences depend non-monotonically on the resource supply point and environmental conditions. Again, this result is independent of the specific properties of $\mathcal{N}^C$ and $\mathcal{F}^C$ but is based on intuitive properties of niche and fitness differences (see Appendix B.1). We also found maxima and minima of niche differences as a function of resource supply. While we were able to show the existence and specific location of such extremes, we know little about their consequences. For example, niche differences are assumed to increase ecosystem function (Carroll *et al.*, 2011; Striebel *et al.*, 2009) or stability with respect to perturbation (Adler *et al.*, 2007). Does this imply that these specific resource supply points produce most function or are most stable?

Third, the non-linear niche differences highlight resource supply points with negative $\mathcal{N}^C$ (Fig. 3.2). At these resource supply points, species have positive frequency dependence, which was unknown for this well-known community model.

3.5.3 Future directions of niche and fitness differences

Recent research has shown that non-linear or higher order species interactions can affect community composition, community stability and coexistence (Grilli *et al.*, 2017; Bairey *et al.*, 2016; Mayfield & Stouffer, 2017). Coexistence theory must therefore move from simple linear models to models including higher order and non-linear interactions (Godoy *et al.*, 2018; Letten & Stouffer, 2019). This can be done by using $\mathcal{N}^C$ and $\mathcal{F}^C$. For example, Spaak *et al.* (2019) analysed the effect of species richness on $\mathcal{N}^C$ and $\mathcal{F}^C$, including models with higher order interactions and showed that higher order interactions affected, on average, $\mathcal{F}^C$, but not $\mathcal{N}^C$. The inclusion of higher order interactions into niche and fitness differences, however, comes at a cost. While the niche and fitness differences computed on a linearisation lead to a simple representation, explicit formulas of niche and fitness differences for the full models are often not possible, making interpretation considerably more complex.

Modern coexistence theory and niche and fitness differences in particular, should *predict* and *understand* species coexistence. However, there are eleven different methods to assess niche and fitness differences, with little consensus about which to use (Spaak & De Laender, 2020). As our results imply, all these different methods can potentially lead to different predictions and explanations of coexistence (Appendix B.4). For example, Song *et al.* (2020a) have shown that a mechanism increasing structural niche differences (Saavedra *et al.*, 2017) may decrease traditional niche differences (Chesson, 1990). Similarly, Song *et al.* (2019) have shown that different methods to asses stabilizing and equalizing mechanisms do not lead to the same understanding of coexistence.

This discrepancy between methods potentially limits out capacity to predict and understand coexistence, as it hampers cross community comparison. We propose to compute niche and fitness differences with multiple methods for the same underlying data. Many methods can be computed with little to no additional effort. Such as Carroll *et al.* (2011), which can be computed based solely on invasion and intrinsic growth rates. Spaak & De Laender (2020) can be computed numerically on most community models and with open software available on `https://github.com/juergspaak/NFD_definitions`. However, we discourage from using methods to assess niche and fitness differences, which do neither correctly predict nor explain species coexistence. We need to compare different methods of niche and fitness differences, both theoretically and empirically, to understand how it affects our capacity to predict and explain coexistence.

Chapter 4

Species richness increases fitness differences, but does not affect niche differences

4.1 Abstract

A key question in ecology is what limits species richness. Modern coexistence theory presents the persistence of species as a balance between niche differences and fitness differences that favour and hamper coexistence, respectively. With most applications focusing on species pairs, however, we know little about if and how this balance changes with species richness. Here, we present the first mathematical proof that, the average fitness difference among species increases with richness, while the average niche difference stays constant. Extensive simulations with more complex models and analyses of empirical data confirmed these mathematical results. Taken together, our work suggests that, as species accumulate in ecosystems, ever-increasing fitness differences will at some point exceed constant niche differences, limiting species richness. Our results contribute to the expansion of modern coexistence theory towards multi-species communities.

4.2 Introduction

Explaining nature's biodiversity is a key challenge for science (Hutchinson, 1957). One type of approach consists of focusing on the capacity of individual species to persist through time despite species interactions and occasional pruning to low density (Turelli, 1978). Modern coexistence theory is such an approach, and predicts species persistence when niche differences overcome fitness differences. Niche differences measure the strength of negative frequency dependence, i.e. whether a focal species i can recover when reduced to low abundance (Chesson, 2000; Adler *et al.*, 2007; Spaak & De Laender, 2020). Fitness differences measure the competitive ability of that species (Hart *et al.*, 2018; Adler *et al.*, 2007; Spaak & De Laender, 2020).

However, few applications of coexistence theory have explicitly focused on explaining biodiversity, i.e. the persistence of species in species-rich communities. Instead, most applications have considered two-species communities (Chesson, 2000; Letten *et al.*, 2017), using a variety of approaches and case studies. For example, niche and fitness differences have been measured in various two-species systems, including annual and perennial plants (Godoy & Levine, 2014; Adler *et al.*, 2018b), phytoplankton (Gallego *et al.*, 2019; Narwani *et al.*, 2013) and bacteria (Zhao *et al.*, 2016), and under different environmental conditions (Bimler *et al.*, 2018; Napier *et al.*, 2016; Matías *et al.*, 2018; Lanuza *et al.*, 2018; Cardinaux *et al.*, 2018; Wainwright *et al.*, 2019; Grainger *et al.*, 2019a). But we found only three empirical studies that report niche and fitness differences in communities composed of more than two species (hereafter multi-species communities) (Veresoglou *et al.*, 2018; Chu & Adler, 2015; Petry *et al.*, 2018). However, none of these three studies explain how niche and fitness differences jointly constrain species richness. In order to understand how niche and fitness differences co-determine species persistence in multi-species communities, we need to understand how both variables change when adding species to a community.

Multi-species communities possess at least four complexities that are absent from two-species communities, which may affect niche and fitness differences, and therefore how both constrain species richness. (i) First, multi-species community can host a multitude of interaction types. Species richness increases the number of possible interactions and the number of combinations of these interaction types. Several metrics exist to summarize this diversity of interaction types and study their implications for community dynamics (Fontaine *et al.*, 2011). (ii) Second, two-species communities are always fully connected and correlations between interspecific interactions (Barabás *et al.*, 2016) become irrelevant since there is only a single pair of interspecific interactions. In contrast, in an n-species community there may be anywhere from $n-1$ to $\frac{n}{2}(n-1)$ connections, and the interspecific effects of species j on species i can be positively or negatively correlated with the interspecific effects i has on j (Barabás *et al.*, 2016). May (1972); Allesina & Tang (2012, 2015) have shown that connectance and correlation can have large effects on the stability of multi-species communities. We therefore expect these factors to influence coexistence as well. (iii) Third, higher-order interactions, through which a third species changes the interaction between a species pair, are by definition absent from two-species communities (but see Letten & Stouffer (2019); Levine *et al.* (2017)). Such higher-order interactions have been found empirically, for example, in communities composed of phytoplankton, bacteria, and ciliates (Mickalide & Kuehn, 2019); in that study, bacteria coexisted with phytoplankton and ciliates, but all three functional groups did not coexist. In the three-species community, phytoplankton inhibited bacterial aggregation, leaving the latter more vulnerable to predation by ciliates. (iv) Fourth, indirect effects, whereby a third species changes the dynamics of a species pair by directly interacting with both partners at the same time, are by definition absent from two-species communities Walsh (2013). We will refer to these four complexities throughout the text with (i) interaction types, (ii) interaction matrix structure, (iii) higher-order interactions and (iv) indirect interactions.

Studying multi-species coexistence is challenging both theoretically and experimentally. Theoretically speaking, the methods to analyse coexistence via niche and fitness differences in a multi-species community were not available until recently (Carroll *et al.*, 2011; Saavedra *et al.*, 2017; Carmel *et al.*, 2017; Spaak & De Laender, 2020). Experimentally speaking, studying coexistence of multiple species is resource-demanding. For instance, in the simple case of linear direct interactions among species (i.e. as in Lotka-Volterra models) the number of experiments needed to parametrize the community is quadratic in species richness (but see Maynard *et al.* (2019)). Considering higher-order interactions will consequently result in an even higher experimental load. For example, measuring higher-order interactions (sensu. Letten & Stouffer (2019)) would require 39 experiments in a three species community.

In this paper we investigate the balance between niche and fitness differences along a gradient of species richness. More specifically, we ask how niche and fitness differences change as the number of species in a community increases, and how the additional complexities (i)-(iv) influence these changes. We do so using four independent methods that rely on a novel definition for niche and fitness differences that is able to analyse multi-species coexistence (Spaak & De Laender, 2020), and a new compilation of species interaction data. First, we derive equations that quantify how niche and fitness differences respond to species richness in a community with linear interactions and simple cases of higher-order interactions. Second, we give an intuitive explanation of these responses based on the Mac-Arthur consumer-resource model. Third, we perform simulations with more complex models. We run these simulations as a full-factorial virtual experiment, varying direct interactions (type, correlation, connectance), indirect interactions, and higher-order interactions. Fourth, we compile data from the literature on empirically measured species interaction matrices and compute niche and fitness differences as a response to species richness. All methods support the same general conclusion: species richness does not affect niche differences, but increases fitness differences. Importantly, these conclusions are independent of the four complexities (i)-(iv).

4.3 Methods

4.3.1 Model and calculation of niche and fitness differences

We use a generalized Lotka-Volterra model with n species containing second-order interactions to model the per-capita growth rates $f_i(N_i, \boldsymbol{N^{-i}})$:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \underbrace{r_i\left(1 + \sum_j \alpha_{ij} N_j \left(1 + \sum_k \beta_{ijk} N_k\right)\right)}_{f_i(N_i, \boldsymbol{N^{-i}})} \tag{4.1}$$

, where N_i is the density of the focal species i, $\mathbf{N}^{-i}$ is the density of the resident community (vector of length $n-1$), r_i is its intrinsic growth rate, and α_{ij} and β_{ijk} are first (or linear) and second-order species interactions, respectively. A positive α_{ij} indicates a positive interaction between species i and j (facilitation). Negative α_{ij} on the other hand indicate negative interactions (competition). When β_{ijk} is positive or negative species k will intensify or weaken the relationship between species i and j, respectively (second-order interaction). The inclusion of third order interactions did not affect any of our results. Throughout the manuscript we assume $\alpha_{ii} = -1$, which can always be achieved by rescaling.

There exist five different definitions to compute niche and fitness differences in multi-species communities (Chesson, 2003; Carmel *et al.*, 2017; Saavedra *et al.*, 2017; Spaak & De Laender, 2020; Carroll *et al.*, 2011). The definitions of Carmel *et al.* (2017) do not apply to the selected model. Chesson (2003) was developed for environmental or spatial fluctuations, which we do not consider here. Saavedra *et al.* (2017) and Carroll *et al.* (2011) do apply to the selected model. However, niche and fitness differences as computed by these two methods allow inference of coexistence only in two-species communities, not in multi-species communities. That is, two different multi-species communities may have identical niche and fitness differences but different outcomes of coexistence (e.g. all species persist in one community, but not in the other). Since we here ask how niche and fitness differences jointly determine coexistence in multi-species communities, these two methods are therefore not applicable here. Consequently, we computed niche and fitness differences as defined by Spaak & De Laender (2020).

Spaak & De Laender (2020) base their definition of niche and fitness differences ($\mathcal{N}$ and $\mathcal{F}$) on the comparison of species growth rates in various conditions. When two species (i and j) have completely separated niches ($\mathcal{N}_i = 1$), the species i will grow in presence of j as it would have in its absence, which implies $f_i(0,N_j^*) = f_i(0,0)$ where $f_i(0,N_j^*)$ is the per capita growth rate of species i when it invades a community with j at equilibrium density N_j^*, known as the invasion growth rate and $f_i(0,0)$ is the intrinsic growth rate of species i. Conversely, if the two species have exactly the same niche ($\mathcal{N}_i = 0$) they have equivalent effects on each other. It then holds that $f_i(0,N_j^*) = f_i(c_jN_j^*,0)$ where c_j is the conversion factor allowing to express individuals of species j as individuals of species i. However, this does not imply, that both species have zero invasion growth rates. Interpolation between these two extreme cases allow defining the niche difference in a two-species community:

$$\mathcal{N}_i = \frac{f_i(0,N_j^*) - f_i(c_jN_j^*,0)}{f_i(0,0) - f_i(c_jN_j^*,0)} \tag{4.2}$$

This definition maps positive frequency dependence, negative frequency dependence and facilitation to $\mathcal{N}_i < 0, 0 < \mathcal{N}_i < 1$, and $1 < \mathcal{N}_i$ respectively.

Similarly, they define fitness differences as the (scaled) growth rate in the absence of niche differences

$$\mathcal{F}_i = \frac{f_i(c_jN_j^*,0)}{f_i(0,0)} \tag{4.3}$$

Zero fitness differences imply that the species have equal competitive strength, as $N_i^* = c_jN_j^*$, competitive subordinate species have negative fitness differences, as $N_i^* < c_jN_j^*$, conversely competitive dominant species have positive fitness differences. This definition can be generalised to a multi-species community (Appendix S1). $\mathcal{N}_i$ and $\mathcal{F}_i$ are species-specific properties, i.e. in general we have $\mathcal{N}_i \neq \mathcal{N}_j$ and $\mathcal{F}_i \neq \mathcal{F}_j$ in multi-species communities. However, $\mathcal{N}$ and $\mathcal{F}$ compare the effect of the focal species on itself to the effect of the rest of the community on the focal species, they therefore do depend on the traits of the other species in the community.

4.3.2 Analyses and Simulations

We first examined analytically how $\mathcal{N}$ and $\mathcal{F}$ change with species richness. We found a generic solution for first-order interactions and for a simplified case of higher-order interactions.

Factor	Parameter	Levels	Interpretation	Complexity investigated
Interaction type first-order	α_{ij}	< 0 > 0 no restriction	competition facilitation mixed	(i)
Strength of interaction first-order	α_{ij}	strong weak		(i)
Connectance	$P(\neq 0)$	$1,\frac{4}{5},\frac{2}{3}$		(ii)
Interaction correlation	$\mathrm{cor}(\alpha_{ij},\alpha_{ji})$ $\mathrm{cor}_{ij}(\beta_{ijk}\beta_{jik})$	1 0 -1	equal unrelated opposite	(ii)
Presence of indirect effects		Yes No	absent present	(iv)
Interaction type second-order	β_{ijk}	> 0 < 0 no restriction $= 0$	intensify weaken mixed no second-order	(i) and (iii)

Table 4.1: Design of full factorial virtual experimental.

Second, we designed a full-factorial virtual experiment in which we numerically computed $\mathcal{N}$ and $\mathcal{F}$ for a wider range of different simulated communities (see table 4.1). For these we solve numerically for equilibrium densities and invasion growth rates using the 'fsolve' function from the scipy package in Python. The factors were (i) first-order interaction type (competitive, facilitative or both, i.e. $\alpha_{ij} < 0, > 0$ or unrestricted); (ii) first-order interaction strength (strong or weak); (iii) connectance of the interspecific interaction ($c \in \left\{1, \frac{4}{5}, \frac{2}{3}\right\}$); (iv) correlation between the interspecific interaction ($\rho(\alpha_{ij}, \alpha_{ji}) = \rho_{ij}(\beta_{ijk}, \beta_{jik}) \in \{-1, 0, 1\}$); (v) inclusion of indirect effects (present or absent); (vi) second-order interaction type ($\beta_{ijk} < 0, > 0$, unrestricted, or absent); To exclude indirect effects we set equilibrium densities of resident species to their monoculture equilibrium density. In this way, we cancel out interactions among residents that will change the residents' densities. The intrinsic growth rate r_i does not affect $\mathcal{N}$ and $\mathcal{F}$, therefore we set it to 1 in all simulations.

This design leads to a total of $3 \cdot 2 \cdot 3 \cdot 3 \cdot 2 \cdot 4 = 432$ parameter settings. We ran 1000 repetitions for each of the five species richness levels ($2 \leq n \leq 6$), leading to a total of $432 \cdot 5 \cdot 1000 = 2'160'000$ simulations. We parametrized the first-order interactions using distributions of empirically obtained first-order interactions (see supplementary informations S2). We sampled "strong" first-order interactions between the $Q_1 - 1.5(Q_3 - Q_1)$ and $Q_3 + 1.5(Q_3 - Q_1)$ of those distributions, where Q_1 and Q_3 are the first and third quartile, respectively. to remove outliers (defined as species interactions outside this range). Similarly, we sampled "weak" first-order interactions between the Q_1 and Q_3 of the empirical distributions of interaction strength. We fitted linear regressions to measure the effect of species richness on $\mathcal{N}_i$ and $\mathcal{F}_i$. With this approach we were able to investigate the effects of all complexities (i)-(iv).

4.3.3 Literature data

We found three review papers that inventoried multi-species Lotka-Volterra interaction matrices (Adler *et al.*, 2018b; Fort, 2018; Keddy & Shipley, 1989), representing a total of 33 interaction matrices, ranging from 3 to 9 species, and containing 29 plant, 2 phytoplankton, 1 zooplankton and 1 ciliate communities. We normalized all these data such that $\alpha_{ii} = -1$. The interaction matrices were obtained through pairwise experiments, measuring the interspecific effect of one species on the other. For each multi-species community we constructed all possible sub-communities with at least two species, leading to a total of 2544 communities that varied in species richness from 2 to 9. We excluded all communities in which not all interaction strengths were available, e.g. because of a "NA" entry in the sampled sub-community, leading to 2296 communities. For 1376 communities we could not compute $\mathcal{N}$ and $\mathcal{F}$. That is because, like any method seeking to quantify frequency dependence, our approach is based on invasion analysis: the capacity of an invader to grow with the other species at their non-zero equilibrium. Thus, one must be able to compute the invasion growth rate of each species, which is the per capita growth rate $f_i(0, \boldsymbol{N}_j^{-i,*})$ when the focal species i is nearly absent (mathematically equal to 0) and the other species are at their equilibrium density $\boldsymbol{N}^{-i*}$. $\mathcal{N}$ and $\mathcal{F}$ are thus only computable for communities where each subcommunity (the community without the invading species) coexists stably. We therefore computed $\mathcal{N}$ and $\mathcal{F}$ for the remaining 920 communities.

For each interaction matrix obtained from the literature we computed $\mathcal{N}$ and $\mathcal{F}$ using equation 4.2 and 4.3. For each of the 33 interaction matrices, we regressed $\mathcal{N}_i$ against species richness of the sub-communities. These data contained many outliers, which skewed the results of our linear regressions. We therefore used a Theil-Sen estimator for the slope, which is more robust to outliers than linear regression based on least squares (Sen, 1968). We fitted (using least squares) a saturating function $\mathcal{F}_i = \frac{n-2}{(n-2)+H}$ for the fitness differences. This saturating response was chosen for $\mathcal{F}_i$, because our analytical results suggested such a response.

4.4 Results

4.4.1 Analytical solutions

For the linear Lotka-Volterra model without higher-order interactions (i.e. $\beta_{ijk} = 0$), we can compute explicitly (see Appendix C.1):

$$1 - \mathcal{F}_i^m = \textstyle\sum_{j,\alpha_{ij}\neq 0}(1 - \mathcal{F}_{ij})\frac{N_j^{-i,*}}{N_j^*} \tag{4.4}$$

$$\mathcal{N}_i^m = \frac{\sum_{j,\alpha_{ij}\neq 0}\left(c_{ij}N_j^{-i,*}\right)\mathcal{N}_{ij}}{\sum_{j,\alpha_{ij}\neq 0} c_{ij}N_j^{-i,*}} \tag{4.5}$$

,where $\mathcal{F}_i^m$ and $\mathcal{N}_i^m$ are the fitness and niche differences of i in the multi-species community (superscript m), $\mathcal{F}_{ij}$ and $\mathcal{N}_{ij}$ are the fitness and niche difference of i in a two-species community consisting of species i and j. c_{ij} is the conversion factor from species j to species i, $N_j^{-i,*}$ is the equilibrium density of species j in the absence of species i and N_j^* is the equilibrium density of species j in monoculture (see methods). The sum is taken across species j with which i interacts directly, i.e. $\alpha_{ij} \neq 0$.

Eq. 4.4 and 4.5 illustrate our two main results. First, $1 - \mathcal{F}_i^m$ is the weighted *sum*, across all species pairs with which i interacts, of the two-species fitness differences $1 - \mathcal{F}_{ij}$.

The weights $\frac{N_j^{-i,*}}{N_j^*}$ are the relative yields, as known from biodiversity ecosystem functioning research (Hector & Loreau, 2001; Fox, 2005). The effect of species richness on fitness differences will therefore be similar to the effect of species richness on the sum of the weights, known as the relative yield total ($\sum_{j\neq i}\frac{N_j^{i-,*}}{N_j^*}$), which is known to increase in many communities (Loreau, 2004; Carroll *et al.*, 2011; Grace *et al.*, 2016). Hence,$1 - \mathcal{F}$ (and therefore of $\mathcal{F}_i$) will on average increase with species richness. Second, $\mathcal{N}_i^m$ is the weighted *average* of the two-species niche overlaps $\mathcal{N}_{ij}$. Hence, species richness will, on average, not affect $\mathcal{N}_i$. Since we did not make assumptions about the α_{ij}, these results are independent of the details of interspecific interactions, i.e. the results apply regardless of complexities (i) and (ii).

We can approximate $\mathcal{N}$ and $\mathcal{F}$ in a multi-species community by using the average interspecific interaction strength $\overline{\alpha}$ (see supplementary informations 1). This yields $\mathcal{N}_i^m \approx 1 - \overline{\alpha}$ and $\mathcal{F}_i^m \approx 1 - \frac{n-1}{1-(n-2)\overline{\alpha}}$, from which it is clear that $\mathcal{N}_i$ is independent of species richness n and $\mathcal{F}_i$ is an increasing but saturating function of species richness. The saturation occurs because the sum of the weights $\frac{N_j^{-i,*}}{N_j^*}$, the relative yield total, will saturate as well in the Lotka-Volterra model (Loreau, 2004; Spaak *et al.*, 2017). Including other complexities does not affect these two main results (Appendix C.1).

4.5 Link to resource competition

The fact that $1-\mathcal{F}_i^m$ is a weighted sum, while $\mathcal{N}_i^m$ is a weighted average makes intuitive sense when realising that the interaction coefficients α_{ij} can under certain conditions be related to resource utilisation (Chesson, 1990; MacArthur, 1970). We consider a focal species (yellow, Fig. 4.1) of a community with one to five resident species (Fig 4.1 A-E), the resource utilisation of each species is given by A_i. We use $\|A_i\|$ to denote the total utilisation rate by the species i, i.e. the area under the curve A_i (Fig. 4.1 F). More generally, for any curve X, $\|X\|$ will denote the area under the curve, that is $\|X\|$ is a number, while X denotes the curve itself. We assume that the species only differ in resource utilisation rates, not in other parameters such as mortality. We want to compute the $\mathcal{N}_1$ and $\mathcal{F}_1$ of the yellow focal species in presence of one up to five competitors.

The species with the higher total utilisation rate will have a competitive advantage and consequently the higher fitness difference. In the two-species community, one could therefore intuit that the fitness differences is linked to the ratio of total resource utilisation rates, i.e. $\mathcal{F}_1 \approx 1-\frac{\|A_2\|}{\|A_1\|}$. Fitness differences therefore increase with species richness, as each competitor increases the total resource utilisation rates of all competitors combined (Fig. 4.1 F), i.e. $\mathcal{F}_1^m \approx 1-\frac{\sum\|A_j\|}{\|A_1\|}$. It turns out that this intuition is almost correct; we only have to add weights to the sum according to the densities of the species at equilibrium (compare this equation to eq. 4.4). $\mathcal{F}_1^m$ thus increases (becomes more negative), as species richness increases (note that $\mathcal{F}_i = 0$ means no fitness differences and more negative $\mathcal{F}_i$ mean stronger fitness differences).

Intuitively, $1-\mathcal{N}_i$ is the proportion of shared resources between the focal species and its competitors, that is the amount of shared resources scaled by the total consumption of the species. In a two species community we therefore intuit $\mathcal{N}_1 \approx 1-\frac{\|A_1\cap A_2\|}{\|A_1\|\cdot\|A_2\|}$. Increasing the species richness will increase both, the sum of shared resources, as the focal species will share resources with each competitor (Fig. 4.1 G) and the sum of the total consumption of the species (Fig. 4.1 F). We therefore expect $\mathcal{N}_1 \approx 1-\frac{\|A_1\cap\sum_j A_j\|}{\|A_1\|\cdot\sum_j\|A_j\|}$ to be independent of species richness (Fig 4.1 H). Again, this intuition is correct up to the inclusion of the weights according to the species equilibrium densities.

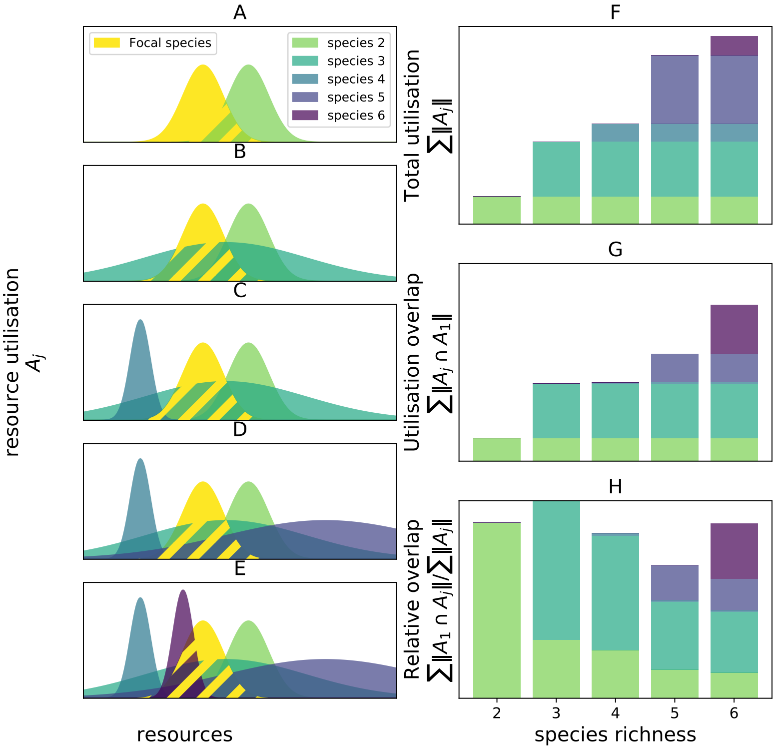

Figure 4.1: A-E: Resource utilisation of the yellow focal species and its competitors. F: Increasing the species richness will increase the total utilisation of the resident species $\sum_j \|A_j\|$. Similarly, we expect $\mathcal{F}_i \approx 1 - \frac{\sum_j \|A_j\|}{\|A_1\|}$ to increase with species richness, as it scales with the ratio of total resource consumption. G: The amount of shared resources (hatched region from panels A-E) increases with species richness. H: As both the amount of shared resources increase (panel G) and the total utilisation (panel H) we expect the ratio to be independent of species richness. Similarly, we expect $\mathcal{N}_i \approx 1 - \frac{\|A_i \cap \sum_j A_j\|}{\|A_i\| \cdot \sum_j \|A_j\|}$ to be, on average, independent of species richness. F-H: The colours of the bar correspond to the contribution of each of the resident species to the total of the bar.

4.5.1 Full-factorial simulations

The simulations with strong first-order interactions only partially seem to confirm the predictions made by theory (Fig. 4.2). That is, $\mathcal{N}_i$ is not invariant but approaches 1 as species richness increases (Fig. 4.2 A), which seems to contradict the theoretical results. Yet, species richness does not directly affect $\mathcal{N}_i$, but rather affects the average interaction strength α_{ij}, which in turn affects $\mathcal{N}_i$. That is because, by design, any method based on invasion growth rates (such as those to compute $\mathcal{N}$ and $\mathcal{F}$) can only be applied to communities in which invasion analysis is possible. Hence, too strong negative interactions prevent the invasion into highly-diverse communities, and will often impede feasible $n-1$ subcommunities to begin with (Kokkoris *et al.*, 2002). Hence, species richness selects against communities with overly strong negative interactions, which leads to on average less strong interactions at higher species richness (see supplementary Fig. S3). Similarly, species densities in communities with strong positive interactions will tend to grow to infinity, and more so in species-rich communities, because interspecific facilitation is stronger than intraspecific limitation (self-regulation). Again, species richness selects against strong positive interactions, weakening the average interaction strength (see supplementary Fig. S3). This selection of weak (negative and positive) interspecific interactions causes $\mathcal{N}_i$ to approach 1. $\mathcal{F}_i$ increases with species richness for all parameter settings, as predicted by the theory (see Fig 4.2 B).

The simulation results based on weak interaction strengths allow assessing the direct effect of species richness on $\mathcal{N}$ and $\mathcal{F}$ without the confounding effect of species richness on interspecific interaction strength α_{ij}. In these simulations, the effect of species richness on interspecific interactions was much weaker (see supplementary Fig. S3). These simulations confirmed our theoretical results; $\mathcal{N}_i$ was on average unaffected by species richness (see Fig. 4.3 A) and $\mathcal{F}_i$ increased with species richness (Fig. 4.3B). We illustrate how $\mathcal{N}$ and $\mathcal{F}$ values jointly varied with species richness, using weak interaction strength: no higher-order interactions ($\beta_{ijk} = 0$), no correlation between the α_{ij}, and maximum connectance (Fig. 4.3 C). Again, these results hold independently of the complexities (Appendix S2).

4.5.2 Literature data

The results for the empirical communities reflect those obtained for the simulated communities. The absolute values of the slope of the linear regression of $\mathcal{N}_i$ were small (< 0.05) for all but 6 datasets. The slope for the overall regression of $\mathcal{N}_i$ against species richness (Fig. 4.4A, black line) was small (-0.028). $\mathcal{F}_i$ increased with richness in all but one dataset. Overall, we conclude that the re-

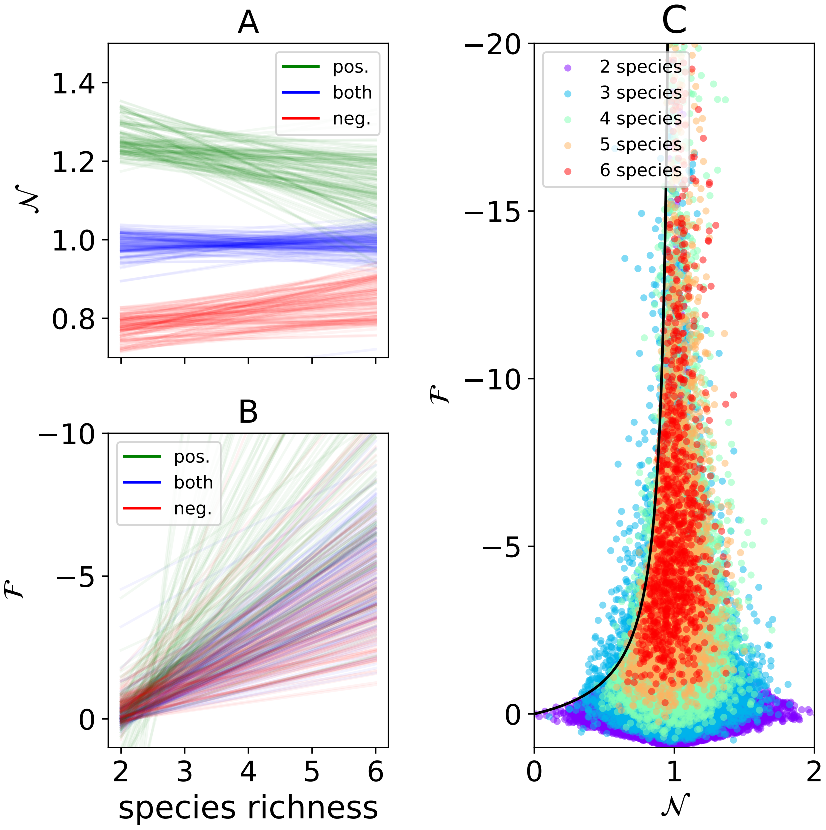

Figure 4.2: $\mathcal{N}$ and $\mathcal{F}$ as a function of species richness in simulated communities with strong first-order interspecific interactions. A: Contrary to predictions from theory, niche differences change with species richness when first-order interspecific interactions are either positive (green) or negative (red; results for unconstrained interspecific interactions are shown in blue). However, this is because interaction strength decreases with increasing species richness in these cases (see Fig. S2). Each line represents a linear regression of niche differences as a function of species richness for one factorial setting of the full-factorial experiment (see table 4.1). B: Species richness, however, makes fitness differences more negative (i.e. larger). Note the differences in y-scale between panel A and B. C: Distribution of $\mathcal{N}$ and $\mathcal{F}$ for simulated theoretical communities that are fully connected, and exhibit first-order interactions without correlations, i.e. similar to the experimental communities (see Fig. 4.4). Each dot represents $\mathcal{N}$ and $\mathcal{F}$ of one species in a community composed of 2-6 species (see colour legend). The black line indicates the persistence line, species below this line are assumed to persist in the community. Note the inverted y-axis.

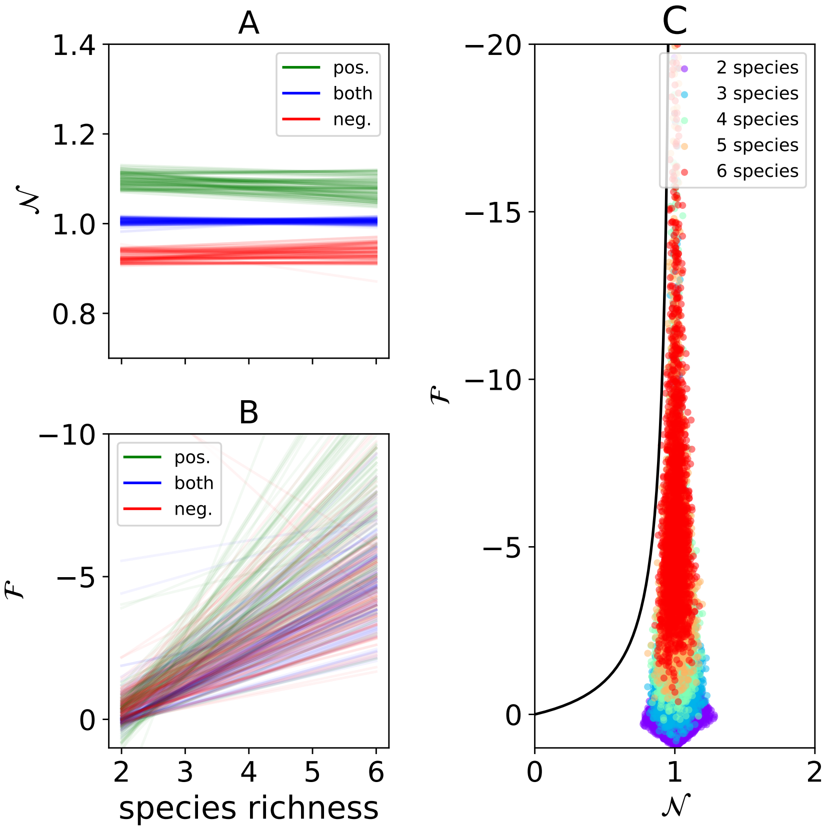

Figure 4.3: As Fig. 4.2, but with weak first-order interspecific interactions. A: As predicted by the mathematical results, species richness does not affect niche differences, because communities with different species richness had comparable interaction strengths. B: Species richness, however, makes fitness differences more negative (i.e. larger). C: Distribution of $\mathcal{N}$ and $\mathcal{F}$ for simulated theoretical communities that are fully connected, and exhibit first-order interactions without correlations, i.e. similar to the experimental communities (see Fig. 4.4).

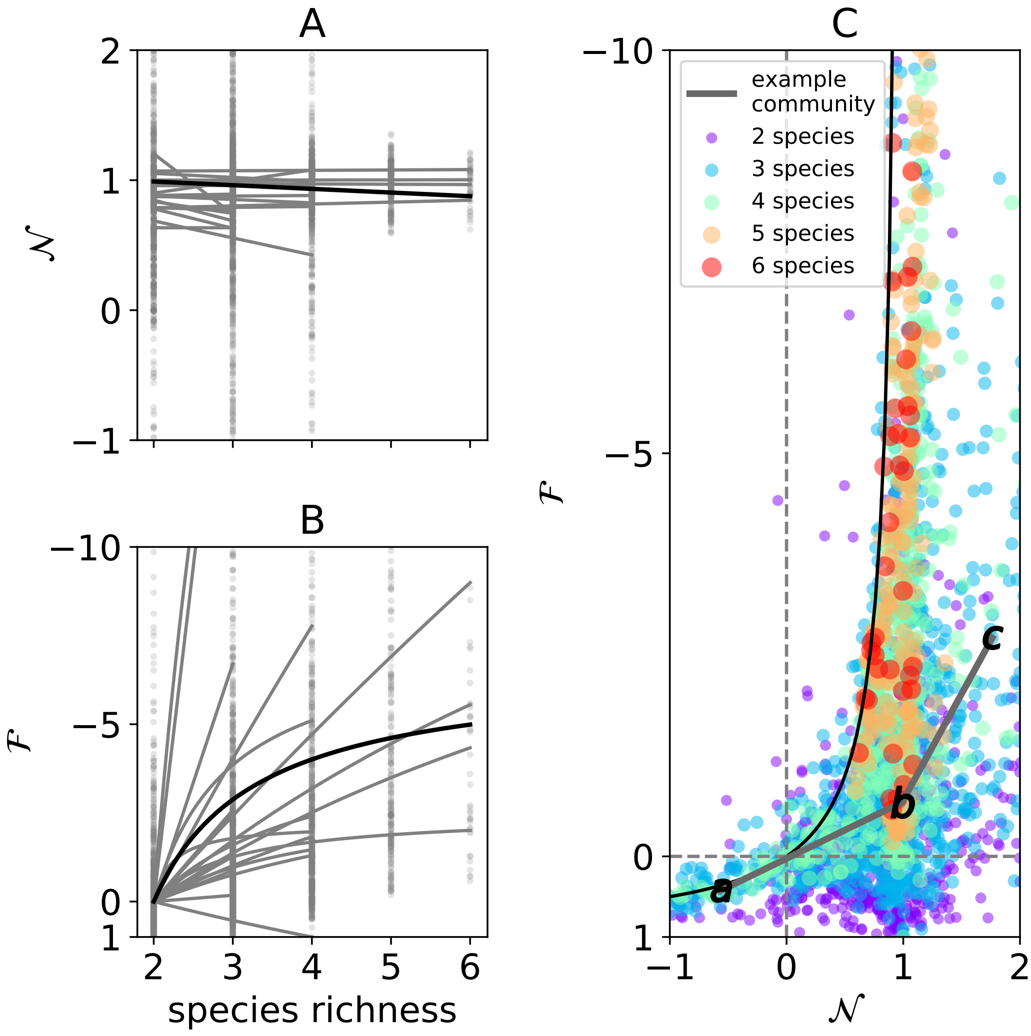

Figure 4.4: Similar to Fig 4.2 for empirically observed communities. Each grey line corresponds to a fit of a linear ($\mathcal{N}_i$, A) and saturating ($\mathcal{F}_i$, B) regression model to one dataset. The black line represents a fit through all $\mathcal{N}_i$ (A) and $\mathcal{F}_i$ (B) values. Grey dots in panel A and B represent the raw $\mathcal{N}$ and $\mathcal{F}$ values. Facilitation, i.e. species having a positive net effect on another, and therefore $\mathcal{N}_i > 1$ is common in the datasets we found. We highlight one specific three-species community (grey line) where all species coexist, even though species *a* has $\mathcal{N}_i < 0$, a property associated with priority effects and therefore exclusion. Axis from C are truncated to show ~95% of all data points.

sponse of $\mathcal{N}$ and $\mathcal{F}$ to richness for empirical communities did not qualitatively differ from that of randomly generated communities.

The empirical data also revealed cases in which coexistence is possible even though some of the species have negative $\mathcal{N}_i$. This is possible as long as $\mathcal{F}_i$ is sufficiently positive such that $\mathcal{F}_i \geq \frac{-\mathcal{N}_i}{1-\mathcal{N}_i}$. A total of 95 (4.1%) communities were found with species persisting despite having negative $\mathcal{N}_i$.

4.6 Discussion

It is well-established that the likelihood for stable coexistence in theoretical communities drops with species richness (May, 1972; Godoy *et al.*, 2017; Goh & Jennings, 1977; Serván *et al.*, 2018). Here, we explain this well known result in the context of modern coexistence theory by examining how niche and fitness differences ($\mathcal{N}$ and $\mathcal{F}$) change with species richness. We found that species richness, *per se*, does not affect $\mathcal{N}_i$ but does increase $\mathcal{F}_i$. This conclusion is based on four independent approaches: mathematical computation, intuitive reasoning, numerical simulations, and metanalysis of experimental data. Overall, the influence of species richness on $\mathcal{N}$ and $\mathcal{F}$ is robust to inclusion or omission of the complexities (i)-(iv), and all their combinations. The fitness differences of a species increases with species richness, as fitness differences measure the fitness of a species compared to the combined fitness of all other species. In multi-species communities, most species will therefore have negative fitness differences, as rarely one species will have higher fitness than all other species combined.

The niche differences of a species measure the proportion of limiting factors, e.g. resources, that are limiting to other species as well. Increasing species richness increases the amount of limiting factors shared with other species, but also the amount of limiting factors that are not shared with other species. The proportion of shared limiting factors is therefore unaffected, on average. Species-rich communities are therefore less likely to coexist (all else being equal), as fitness differences become to strong to be overcome by niche differences.

These results appear to contradict what has been suggested by Chu & Adler (2015). Indeed, in their discussion, Chu & Adler (2015) found that species richness will decrease niche differences and will not affect fitness differences. However, the use of different definitions for $\mathcal{N}$ and $\mathcal{F}$ explains this difference (Carroll *et al.*, 2011). Applying the same definition to our data indeed reproduces the results found by Chu & Adler (2015) (see supplementary informations S4). Yet, we argue that our results provide a more complete and accurate account of how $\mathcal{N}$ and $\mathcal{F}$ limit multi-species coexistence because of the following reasons. First, the definition of Spaak & De Laender (2020) does not only consider negative frequency dependence, but also positive frequency dependence and facilitation. The definition of Carroll *et al.* (2011) can only be computed for communities with negative frequency dependence, which precludes the analysis of 75% of the empirical data analysed in the present chapter and 67% of the simulated data presented here. Second, the $\mathcal{N}$ and $\mathcal{F}$ as defined by Spaak & De Laender (2020) link to the persistence of species via the equation $-\mathcal{F}_i \leq \frac{\mathcal{N}_i}{1-\mathcal{N}_i}$. Again, this is not the case for the definition by Carroll *et al.* (2011) in multi-species communities. Since we are not only interested in how $\mathcal{N}$ and $\mathcal{F}$ change with species richness, but also in the implications of such changes for coexistence, the definition of Carroll *et al.* (2011) is not sufficient. Third, Spaak & De Laender (2020) show that $\mathcal{N}_i$ is biologically intuitive as it measures the amount of shared resources in a large class of resource competition models. Fig.4.1 extends this intuitive explanation to multi-species communities.

4.6.1 Limitations

The available experimental data only represented fully connected communities, with no correlation among interactions (complexity (ii)) and, most notably, did not contain cases of higher-order interactions (complexity (iii)). We do therefore not know whether the parameter values used to describe these higher-order interactions in our simulations (and therefore the simulation results) are realistic. The available experimental data were biased towards competitive communities of terrestrial plants with relatively low species richness. Our simulations suggest that our conclusions hold for other networks as well, but we were not able to support this claim with empirical data. Computing $\mathcal{N}$ and $\mathcal{F}$ on a larger collection of natural communities would help to refine our understanding of this process. However, obtaining the full interaction matrix for species-rich communities is challenging. To obtain interaction matrices, various approaches exist. For example, one uses the frequency of interaction between species (e.g. number of visits of a pollinator on a plant) as a proxy for interaction strength. The robustness of this approach, however, still needs to be tested (García-Callejas *et al.*, 2018). Other methods consist of estimating interaction strength based on, for example, biomass (Moore *et al.*, 1996; Zhao *et al.*, 2019), mass ratio (Emmerson & Raffaelli, 2004) or production and consumption rates of species (Christensen V. & D., 1992; Jacquet *et al.*, 2016). These different methods rely on different assumptions and may therefore influence the resulting matrix estimate (Carrara *et al.*, 2015).

Given these limitations, one can ask to what extent addressing them would change our conclusions. In communities where species richness increases total abundance, which is the case for various communities (Loreau, 2004; Turnbull *et al.*, 2013; Grace *et al.*, 2016), we expect the no-niche growth rate $f_i(\sum_j c_{ij} N_j^{-i,*}, 0)$ to become more negative, as $\sum_j c_{ij} N_j^{-i,*}$ increases (eq. 4.2, 4.3). Consequently we expect species richness to increase fitness differences, i.e. make it more negative. Conversely, in communities where species richness decreases total abundance we expect the opposite, that is: fitness differences might decrease with species richness. It is less clear how species richness will affect niche differences in models not explored in the current chapter, e.g. with different per-capita growth rates, or with a community with age structure (Chu & Adler, 2015). Niche differences depend on the invasion growth rate and the no-niche growth rates, which both depend on the species richness and total abundance. When species richness has a stronger negative effect on the no-niche growth rate than on the invasion growth rate, then niche differences will increase with species richness. If the invasion growth rate is affected more, niche differences will decrease.

4.6.2 New insights

Our results yield two new insights, other than the main result on how $\mathcal{N}$ and $\mathcal{F}$ varies with species richness.

A first insight is that negative niche differences do not necessarily preclude coexistence. Negative niche differences have been attributed to priority effects and therefore viewed as precluding coexistence (Ke & Letten, 2018; Fukami *et al.*, 2016). Our framework confirms this finding for the case of competitive two-species communities (Spaak & De Laender, 2020). However, in contrast to species in two-species communities, species in multi-species communities will not all have the same niche differences (example community in Fig 4.4). This implies that species a, with negative niche differences and low fitness differences, can coexist with species b and c that have positive niche differences and negative fitness differences. Consequently, multiple species can have negative niche differences in a multi-species communities and still persist. In our empirical data set, we found six three-species communities in which all but one species had negative niche differences. In general, we argue that a community in which all species have negative niche differences and coexist is theoretically possible. However, the kind of model and how it should be parametrized remains to be examined.

A second and main insight is that one can infer $\mathcal{N}$ and $\mathcal{F}$ in multi-species communities from $\mathcal{N}$ and $\mathcal{F}$ measured in pairwise interaction experiments. If one measures $\mathcal{N}$ and $\mathcal{F}$ for each two-species sub-community of an n species community, which is typically done (Narwani *et al.*, 2013; Godoy & Levine, 2014; Petry *et al.*, 2018; Gallego *et al.*, 2019), one can estimate $\mathcal{N}_i \approx \frac{\sum_j \mathcal{N}_{ij}}{(n-1)}$. With one additional multi-species experiment to estimate the relative yield RY_i we obtain an estimation of $\mathcal{F}_i \approx 1 - \sum_j (1 - \mathcal{F}_{ij}) \cdot \mathrm{RY}_j$ as well. This indicates that two-species experiments are sufficient to predict $\mathcal{N}$ and $\mathcal{F}$ in multi-species communities.

Finally, one of the key questions in community ecology is whether niche differences are strong enough to overcome fitness differences and allow coexistence. Often, niche differences are found to be not only sufficiently strong, but much stronger than strictly needed Levine & HilleRisLambers (2009); Chu & Adler (2015). The present results offer a potential explanation for this observation. That is, niche differences not only need to be sufficiently strong to overcome fitness differences of one or few competitors, as typically considered in empirical studies, but sufficiently strong to overcome fitness differences of the entire resident community, as niche differences is independent of species richness. Our results therefore allow asking the more general question of how many species one can pack in a community, given its niche difference.

Chapter 5

Unimodal effects of pigment richness on niche and fitness differences explain species richness and ecosystem function in light-limited phytoplankton communities

5.1 Abstract

Trait diversity is traditionally seen as promoting species richness and ecosystem function. Species with dissimilar traits would partition available resources, increasing niche differences, facilitating coexistence and increasing ecosystem function. Here we first show, using theory and simulations for light-limited phytoplankton, that combing photosynthetic pigments is indeed a necessary condition for coexistence and stimulates ecosystem function. However, pigment richness does mostly not permit the coexistence of more than two species, and increases productivity at most 60% compared to single-pigment communities. Surprisingly, combining all nine pigments known to date leads to a 2.5% probability that four species would coexist, illustrating that the coexistence of a high number of species along a continuous niche axis is constrained by limiting similarity. We explain these constraints by unimodal effects of pigment richness on niche and fitness differences, which jointly limit the positive effect of pigment on species richness. Empirical data and additional simulations suggest that pigment richness effects can be stronger during transient dynam-

ics but inevitably weaken with time, i.e. pigment richness effects on species richness and function are likely short-lived. Our results highlight the need to apply coexistence theory to understand the long-term effects of trait diversity on biodiversity and ecosystem function.

5.2 Introduction

Species richness is a main predictor of ecosystem function and stability (Hector & Loreau (2001); Hooper *et al.* (2005) but see Spaak *et al.* (2017); Srivastava & Vellend (2005)). Communities with more species typically produce more biomass and more stably do so than communities with few species (Striebel *et al.*, 2009; Tilman, 1996; Hector & Loreau, 2001; Balvanera *et al.*, 2006). Thus, identifying the factors that sustain and limit the capacity of species to coexist is an essential task, and probably one of the most fundamental objectives in ecology (Chase & Leibold, 2003; Hubbell, 2001; Chesson *et al.*, 2001; Tilman, 1982).

In the past three decades of community ecology, traits have been considered a key ingredient to explain species coexistence (Mcgill *et al.*, 2006; HilleRisLambers *et al.*, 2012). Traits determine both how species respond to environmental variation and to the presence of other species (Chase & Leibold, 2003) and it is generally accepted that trait diversity drives niche differences, which act to stabilize coexistence (McKane *et al.*, 2002; Mayfield & Levine, 2010). Indeed, when all species have identical traits, trait diversity is zero and stable coexistence is not possible (Chesson, 2000; Bell, 2000; Hubbell, 2001). In addition, trait diversity allows coexisting species to exploit a more diverse set of resources and do so more completely, optimising function.

Recent progress in coexistence theory has shown that trait diversity can have both positive and negative effects on biodiversity, including species richness. That is because, apart from increasing stabilizing niche differences, trait diversity can also increase fitness differences (HilleRisLambers *et al.*, 2012; Gallego *et al.*, 2019; Narwani *et al.*, 2013), which can act to disrupt coexistence when they overrule the stabilizing effects. Whether trait diversity supports or limits the number of species that can stably coexist, and thus biodiversity, is therefore unsure (Violle *et al.*, 2011; Best *et al.*, 2013; Levine & HilleRisLambers, 2009). Do species coexist because they are sufficiently different or because they are sufficiently similar?

Here, we theoretically investigate the effects of trait diversity (the number of different traits, i.e. trait richness) on the number of stably coexisting species, niche and fitness differences and ecosystem function (total biovolume). Our working hypothesis was that a greater trait richness would lead to higher species richness and function because it would increase niche differences more than fitness differences, corresponding to prevailing ideas on the effects of trait richness. We considered light limited phytoplankton communities as a globally relevant study system that drives most aquatic food-webs. (Field *et al.*, 2009; Irigoien *et al.*, 2004; Striebel *et al.*, 2012; Baggio *et al.*, 2018; Kulkarni & De Laender, 2017). Competition for light in phytoplankton communities is a major process explaining community composition throughout the world's aquatic habitats (Goldman *et al.*, 1979; Langdon, 1988; Stomp *et al.*, 2007a). Phytoplankton communities in meso- and eutrophic lakes and oceans, where light is the main limiting factor, produce approximately 30%-40% of the world's annual primary production (Field *et al.*, 2009; Berger *et al.*, 2006; Boyd, 2002). In addition, competition for light is particularly suitable to test our expectations because the light spectrum represents a continuous resource axis, which a high number of species could in principle be able to partition.

The traits involved in competition for light are pigments and photosynthetic efficiency, i.e. the amount of biovolume gained per absorbed photon (Huisman & Weissing, 1994; Stomp *et al.*, 2004). Differences of pigmentation phenotypes have been shown to facilitate coexistence among, for example, cyanobacteria species (Stomp *et al.*, 2004, 2007a). Pigment diversity is also expected to allow a more complete utilisation of the light spectrum (Striebel *et al.*, 2009), thus promoting both species richness and optimizing function. Photosynthetic efficiency alone cannot facilitate coexistence, the reason for which we do not consider this trait further.

We start this paper by theoretically examining how pigment richness determines the number of stably coexisting phytoplankton species and ecosystem function (total biovolume). We do so by analysing a phytoplankton growth model that incorporates the partitioning of the light spectrum among species with different pigments (Stomp *et al.*, 2004). We show that, when all species share one pigment, communities evolve to mono-dominance. When a community contains multiple of the main nine photosynthetically active pigments found in nature, up to four species coexist based on light spectrum partitioning, but with low probability. We explain this result through unimodal effects of pigment richness on niche and fitness differences. Higher pigment richness also increases total biovolume by approximately 60%.

Next, we compile data from the literature and find a much stronger positive effects of pigment trait richness on species richness and ecosystem function. We reconcile these data with additional model simulations, finding that the reported effects are likely short-lived (transient) phenomena. Our findings highlight that applying coexistence theory is needed to understand the mechanisms linking species richness to ecosystem functions on time scales relevant for natural systems.

5.3 Methods

5.3.1 Model description

We used a model proposed earlier by Stomp *et al.* (2004), which is equivalent to (Appendix D.1):

$$\frac{dN_s}{dt} = \phi_s \int_{400}^{700} \frac{N_s k_s(\lambda)}{\mathrm{abs}(\lambda)} \cdot I_{in}(\lambda) \left(1 - e^{-\mathrm{abs}(\lambda)}\right) d\lambda - lN_s \tag{5.1}$$

Where N_s is the density of species s (in fl/ml), ϕ_s is the photosynthetic efficiency, $k_s(\lambda)$ is the absorption spectrum of species s, $\mathrm{abs}(\lambda) = z_m \cdot (k_{BG}(\lambda) + \sum_{i=1}^{n} k_i(\lambda)N_i)$ is the sum of all absorbers (background and phytoplankton species), where k_{BG} is the background absorption, z_m is the mixing depth and n is the species richness, $I_{in}(\lambda)$ is the incoming light intensity and l is the loss rate. Note that we considered the loss rate not as a species-specific parameter but rather the dilution rate of the system. The integral is taken over the whole range of photosynthetic active radiation (400nm - 700nm).

$I_{in}(\lambda)\left(1 - e^{-\mathrm{abs}(\lambda)}\right)$ can be thought of as the total amount of photons absorbed by the system and $\frac{N_s k_s(\lambda)}{\mathrm{abs}(\lambda)}$ is the fraction of these photons that species s uses for its growth.

5.3.2 Analyses and simulations

We used equation 5.1 to examine how trait (pigment) richness affects species richness and ecosystem function. We first theoretically analysed the maximum number of species that can stably coexist based on a predefined number of pigments.

Next, we ran simulations to determine the actual number of species and level of ecosystem function corresponding to a given pigment richness. To do so first, we collected 15 algal pigmentation types from the literature representing the major pigmentations of marine and freshwater phytoplankton (Six *et al.*, 2007; Van Den Hoek *et al.*, 1995) (Appendix D.2). Then, we randomly assembled 400‘000 communities composed of a random number of species (1 to 15). In every community, every species was randomly assigned a pigmentation type. The absorption spectrum of a species is defined as the sum of it's pigments:

$$k_s(\lambda) = \sum_p \alpha_{s,p} k_p(\lambda) \tag{5.2}$$

Where k_s is the absorption spectrum of the species, k_p is the absorption spectrum of the pigment and $\alpha_{s,p}$ is the concentration of pigment p in species s. The identity of the pigments present in a species is given by its pigmentation type. The absorption spectra of the pigments ($k_p(\lambda)$) were taken from the literature (Bricaud *et al.*, 2004; Six *et al.*, 2007). Fig. 5.1 B,C shows an example for two pigmentation types. The total absorption of each species was kept constant ($\int_{400}^{700} k_s(\lambda) d\lambda = 2 \cdot 10^{-7} cm^{-1} fl^{-1}$), to avoid species with more pigments absorbing more light. Furthermore, we varied the photosynthetic efficiency ($1.0 \cdot 10^6 \frac{fl}{\mu mol\, photons} \leq \phi_s \leq 3.0 \cdot 10^6 \frac{fl}{\mu mol\, photons}$) (Langdon, 1988), the dilution rate ($0.003h^{-1} \leq l \leq 0.015h^{-1}$) (Stomp *et al.*, 2004; Striebel *et al.*, 2009) and the incoming light intensity ($20 \mu mol\, photons\, m^{-2} s^{-1} \leq I_{tot} \leq 200 \mu mol\, photons\, m^{-2} s^{-1}$) (Stomp *et al.*, 2004; Striebel *et al.*, 2009). We assumed that the background absorption is negligible ($k_{BG} \approx 0$, Appendix D.3 for simulation with non-zero background absorption).

For every community we measured species richness, pigment richness and ecosystem function over time. To measure species richness and pigment richness we assumed that species with relative densities below 0.01% are extinct. Changing this threshold to 1% or 0.0001% did not change our results. The ecosystem function we considered was total biovolume ($EF = \sum_{i=1}^{n} N_i$). The ecosystem function was measured in communities with intensity of incoming light fixed at $40 \mu mol$ photons $m^{-2} s^{-1}$. Again, changing this value to $20 \mu mol$ photons $m^{-2} s^{-1}$ or $80 \mu mol$ photons $m^{-2} s^{-1}$ did not qualitatively alter the results.

For each community at equilibrium we computed the niche and fitness differences ($\mathcal{N}$ and $\mathcal{F}$) of the persisting species, using the definition Spaak & De Laender (2020). Technically, Spaak & De Laender (2020) define $\mathcal{N}_i$ based a species i's growth rate under various conditions, including its invasion growth rate (i.e. its growth rate when seeded in a community of other species) and its intrinsic niche growth rate (i.e. at low density in absence of competitors). As the difference between the invasion and intrinsic growth rate gets larger, $\mathcal{N}_i$ will approach zero, which indicates strong species interactions. In the current context, we expect this to correspond to the case where species have identical pigmentation, and thus compete maximally for light. Conversely, as the difference between the invasion and intrinsic growth rate gets smaller, $\mathcal{N}_i$ will approach one, which indicates weak species interactions. We expect this to correspond to the case where species differ markedly in pigmentation. Spaak & De Laender (2020) define $\mathcal{F}_i$ as the growth rate of species i in absence of niche differences, scaled by the intrinsic growth rate of species i. In that case, the species with the highest scaled growth rate has the largest fitness difference. Because these definitions do not lead to closed forms of $\mathcal{N}$ and $\mathcal{F}$, we computed $\mathcal{N}$ and $\mathcal{F}$ numerically.

5.3.3 Literature data

We searched the literature for experimental data describing the effects of pigment richness on species richness and ecosystem function. We used the search term (phytoplankton OR algae) AND ("pigment richness" OR "pigment diversity") AND ("ecosystem function" OR biodiversity) using the search engines scopus and google scholar. Additionally, we screened all papers cited by or citing as such identified papers. We identified four datasets (two representing field samples from freshwater lakes and two representing experiments with freshwater and marine phytoplankton respectively). The two field data sets represent different sampling locations in one lake (Fietz & Nicklisch, 2004) and from multiple lakes (Striebel, personal communications), respectively. The experimental dataset of Estrada *et al.* (2004) represents phytoplankton diversity in solar salterns with salinity ranging from 4% to 22.4%. We excluded salinities above 22.4%, as they do not resemble marine ecosystems (Estrada *et al.*, 2004). Striebel *et al.* (2009) assembled 1 to 10 species of freshwater phytoplankton and measured pigment richness and ecosystem function after 14 days. Pigment richness was measured using high-performance liquid chromatography in all datasets. The datasets contain more pigments, as they include the pigments used for photo protection. For every dataset, we linearly regressed the log transformed species richness and log transformed biovolume against pigment richness, and compared it with the theoretical results.

The empirical data we found differs in two aspects from our simulated data. First, our simulated data represent long-term effects of pigment richness on species richness and function under steady environmental conditions and it is not sure if the empirical data likewise represent such long-term effects. The field communities will have been exposed to environmental fluctuations and the experimental communities were observed during relatively short-term experiments (8-14 days). Second, the empirical data contain photosynthetic pigments as well as non-photosynthetic pigments, typically used for photoprotection. We therefore repeated our simulations, breaking them off after 10 days, hence simulating the time window typically adopted by experiments. We also included six non-photosynthetic active pigments, that absorb light, but do not contribute to growth (Bricaud *et al.*, 2004). Specifically we changed $\text{abs}(\lambda) = z_m \cdot \left(k_{BG}(\lambda) + \sum_i (k_i(\lambda) + k_i^p(\lambda))N_i\right)$ from equation 5.1, where $k_i^p(\lambda)$

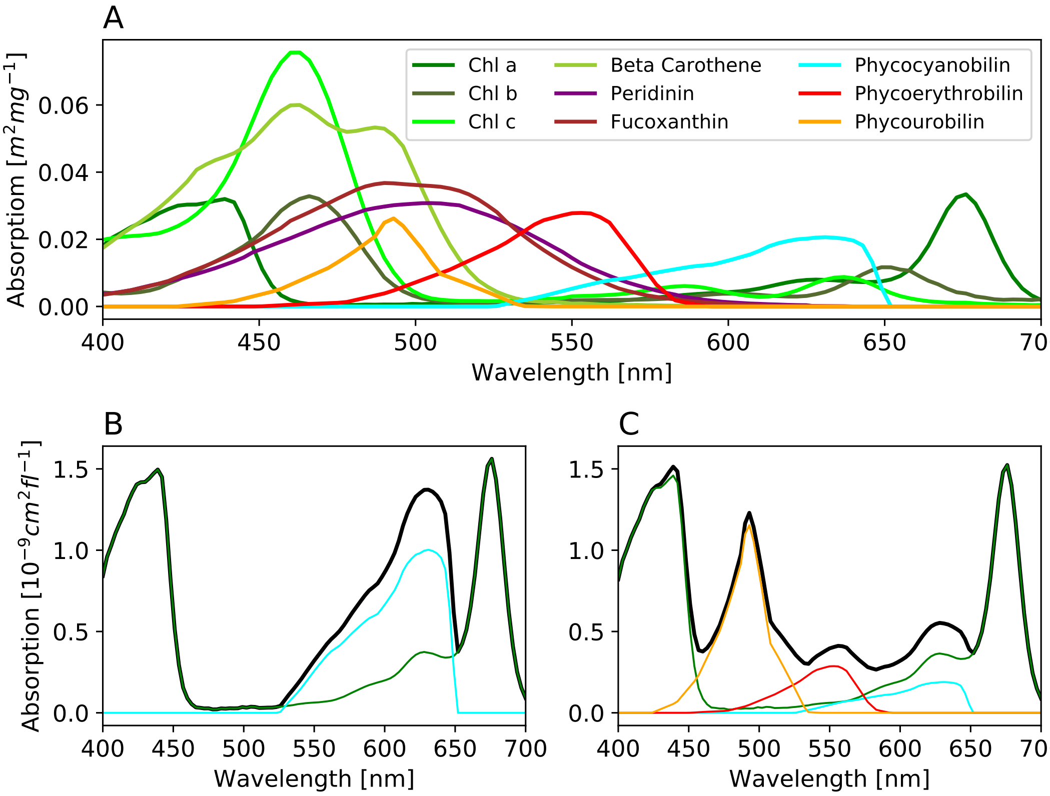

Figure 5.1: In vivo absorption spectra of all considered pigments (A) and two examples (B: Cyanobacteria type 1, C: Cyanobacteria type 3) showing how absorption spectra (black) can be decomposed into different pigments (Eq. 5.2). The two species in B and C can coexist under white light, as the Cyanobacteria type 1 is a superior absorber in the red light (620-700 nm), while the Cyanobacteria type 3 species is a better absorber in the blue-green light (450-550 nm).

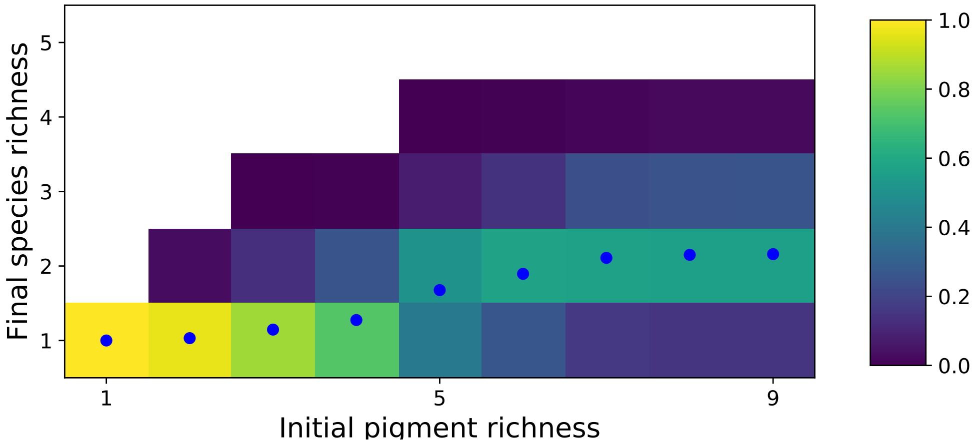

Figure 5.2: Final species richness depends only weakly on the initial number of pigments. Colours denote the probability associated with these species richness levels. Blue dots show the average of the final species richness.

is the combined absorption spectra of the photo protective pigments. $k_i^p(\lambda)$ was generated similar to $k_i(\lambda)$.

5.4 Results

5.4.1 Effects of pigment richness on coexistence

We found that one can decompose the growth rate of a species as:

$$\frac{1}{N_s}\frac{dN_s}{dt} = \phi_s \sum_p \alpha_{s,p} \Psi_p(N) - l \tag{5.3}$$

$$\Psi_p(N) = \int_{400}^{700} \frac{k_p(\lambda)}{\text{abs}(\lambda)} \cdot I_{in}(\lambda) \left(1 - e^{-\text{abs}(\lambda)}\right) d\lambda \tag{5.4}$$

Where $\Psi_p(N)$ is the amount of light absorbed by pigment p. Stable and feasible coexistence, i.e. all species have non-zero equilibrium densities, would impose $\frac{dN_s}{dt} = 0$ for all the species s. This yields a linear equation in the variables $\Psi_p(N)$. This equation can only have a solution if the number of species is at most equal to the number of pigments in the community. This finding proves the fact that species richness is limited by pigment richness for constant incoming light intensity (Meszéna *et al.*, 2006).

These new analytical results show that the number of pigments puts an upper bound on the number of coexisting species, but how many coexisting species can we on average expect at a given number of pigments? While equation 5.3 will always have a solution, this solution might not be ecologically possible. For example, all pigments should have a positive contribution to growth ($\Psi_p(N) > 0$). In addition, pigments in nature often share peaks: Many pigments have maxima in the blue part of the spectrum ($400nm - 450nm$) such that the different $\Psi_p(N)$ are not independent functions (Fig. 5.1 and Stomp *et al.* (2007a)).

Our simulations of species richness at various combinations of pigment richness and photosynthetic efficiencies show that the number of coexisting species is often lower than the number of pigments. Initial pigment richness increased average species richness from 1 to 2.2 (Fig. 5.2). When all pigments are present (initial pigment richness = 9), at most 4 species can coexist, but with low probability ($\approx$ 2.5%). We repeated the analysis with several alternative assumptions on initial species richness (ranging from 1-25), the included pigments (including carotenoids with photo-protective purposes), the absorption spectrum of the pigments, the presence of pigments in species, the absorption spectrum of the background and the incoming light spectrum (appendix D.3). We also ran simulations in which absorption spectra of pigments where randomly generated and pigments were randomly distributed to species. All of these simulations lead to the same main conclusion: pigment richness is essential to allow coexistence but does mostly not allow the coexistence of more than two species in light limited phytoplankton communities.

We identified three reasons for this result, all related to how pigment richness affect niche ($\mathcal{N}_i$) and fitness differences (FD_i). First, pigment richness had a unimodal effect on $\mathcal{N}_i$ (Fig. 5.3 A). At low pigment richness, pigment richness increases $\mathcal{N}_i$, as it increases the probability species will be coloured differently, which stimulates light partitioning. As pigment richness increases, however, species tend to contain an increasing number of pigments, blurring differences in pigmentation, which reduces $\mathcal{N}_i$. Second, pigment richness does not only affect $\mathcal{N}_i$, which benefits coexistence, but also increases differences among species' $\mathcal{F}_i$, which hampers coexistence. Intermediate pigment richness lead to clear competitive dominant (high $\mathcal{F}_i$) and subordinate (low $\mathcal{F}_i$) species (Fig 5.3 B). Communities with intermediate pigment richness will contain species with many pigments, that absorb most wavelengths and have high fitness, and species with few pigments, that absorb only part of the wavelength and have low fitness. The difference in these fitnesses leads to large $\mathcal{F}_i$, both positive and negative. As pigment richness increases all species become generalists and have high fitness, therefore $\mathcal{F}_i$ are closer to zero. Third,

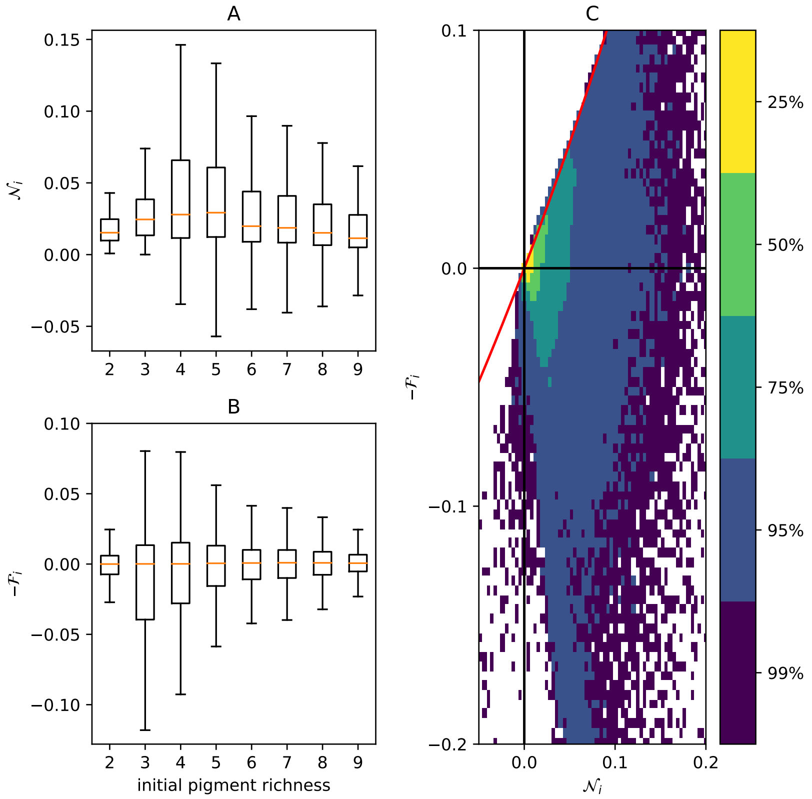

Figure 5.3: A: Pigment richness has a unimodal effect on $\mathcal{N}_i$. Initially multiple pigments allow niche differentiation by the use of different wavelength. However, this positive effect of pigment richness on species richness is limited to few pigments (up to about 4 pigments) and generates only small $\mathcal{N}_i$ compared to empirical measurements in phytoplankton (Narwani *et al.*, 2013; Gallego *et al.*, 2019). At higher pigment richness the species tend to be more generalists and absorb multiple wavelengths, which reduces pigment richness. Shown are the 5, 25, 50, 75 and 95 percentiles of $\mathcal{N}_i$ of all persisting species from all simulated communities. B: Similarly, pigment richness affects $\mathcal{F}_i$. Communities with intermediate pigment richness are composed of species with many pigments, that have high fitness, and species with few pigments, that have low fitness, leading to both, strong negative and positive $\mathcal{F}_i$. The species with strong negative $\mathcal{F}_i$ are most vulnerable to exclusion. Communities with low or high pigment richness are composed of species with few or many pigments, respectively. The species from these communities tend to have similar fitness, which leads to weak $\mathcal{F}_i$. C: Two-dimensional histogram of $\mathcal{N}$ and $\mathcal{F}$ for all species in all communities, independent of their pigment richness. Most species have both $\mathcal{N}_i$ and $\mathcal{F}_i$ close to 0. Shown are the 25,50,75, 95 and 99 percentiles of the distribution, e.g. 25% of the species have $\mathcal{N}$ and $\mathcal{F}$ within the yellow area. Species below the red-line have a positive invasion growth rate, i.e. they are assumed to persist.

$\mathcal{N}$ and $\mathcal{F}$ were located close to the origin of the $\mathcal{N}$ and $\mathcal{F}$ plane (Fig. 5.3 C), showing that different pigmentation types only offered limited opportunity for differentiation among species. This is explained by all pigmentation types containing chlorophyll a, which makes pigmentation more similar (Appendix D.2, Van Den Hoek *et al.* (1995)), and different pigments having similar absorption spectra (Stomp *et al.*, 2007a). Again, repetition of the simulations with altered parameters led to the same results, niche and fitness differences are located close to the origin in the $\mathcal{N}$ and $\mathcal{F}$ plane (Appendix D.3).

Contrary to our theoretical results, the compiled empirical data did suggest a strong positive effect of pigment richness on species richness (Fietz & Nicklisch, 2004; Estrada *et al.*, 2004; Striebel *et al.*, 2009). However, our model analyses and simulations represent the long-term outcome of species interactions in stable environmental conditions, while the empirical data describe experiments performed on much shorter time scales (approximately 10 days) and natural communities with unknown environmental conditions. Thus, the empirical data potentially describe communities that are in a transient state, heading towards lower levels of species richness. Our additional model simulations of short-term effects of pigment richness on species richness indeed suggest time scale to be an important explanation for the difference between our model results and the empirical data. These simulations showed that effects of initial pigment richness on species richness are indeed initially strong, but become weaker over time: pigment richness promoted short-term species richness (Fig. 5.4A).

5.4.2 Implications for ecosystem function

Our simulations show that ecosystem function in communities with high pigment richness is up to 60% higher than in communities with low pigment richness (total biomass, Fig. 5.4B). This increase of ecosystem function is mainly due to selection effect and not complementarity (Appendix D.4). Complementarity is low, because light partitioning allows only limited niche differentiation. As found for species richness, the compiled empirical data did suggest a stronger positive effect (larger slope) of pigment richness on ecosystem function (Striebel *et al.*, 2009; Estrada *et al.*, 2004; Fietz & Nicklisch, 2004) (Fig. 5.4). Again, we additionally simulated short-term effects of pigment richness on ecosystem function (Fig. 5.4B, light green) and found a stronger effect of pigment richness on ecosystem function than for communities at equilibrium (dark green). The effects of initial pigment richness on function are initially strong but dampen with time.

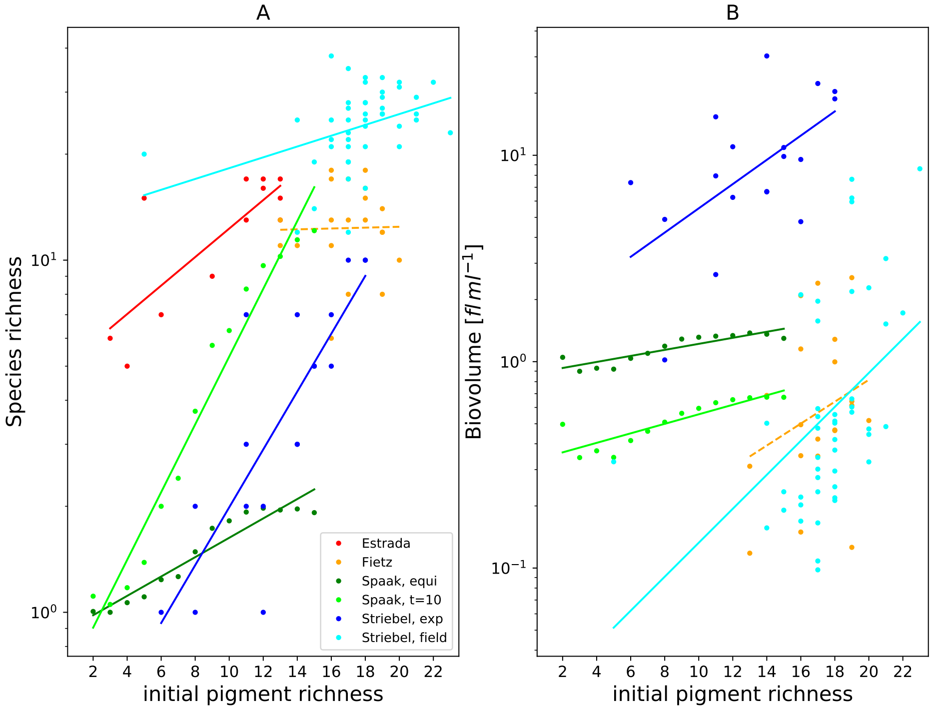

Figure 5.4: Empirical effect of initial pigment richness on species richness (A) and ecosystem function (biovolume B). A: Effects of pigment richness on species richness is initially strong (light green line), but weakens as the communities approach equilibrium densities (dark green line). Similarly, empirical data report a positive effect of pigment richness on species richness. This positive effect is stronger in experimental datasets (dark blue and red) than in natural communities (light blue and orange), presumably because natural communities are closer to equilibrium densities than short term experiments. B: The same observations hold true for the effects of pigment richness on ecosystem function, these are initially strong (slope of light green: 0.101 ± 0.012), but weaken over time (slope of dark green: 0.063 ± 0.007). Dashed lines indicate, that slope did not significantly differ from 0 (i.e. $p > 0.05$).

5.5 Discussion

In the past decade, ecology has evolved towards trait based approaches, as species interactions are governed through species traits and not through species identities (Litchman & Klausmeier, 2008; Mcgill *et al.*, 2006; Degen *et al.*, 2018). Trait based approaches have been used to explain species richness (Violle *et al.*, 2011; Best *et al.*, 2013), coexistence mechanisms such as niche and fitness differences (Kraft *et al.*, 2015; Narwani *et al.*, 2013; Gallego *et al.*, 2019), and ecosystem function (Gross *et al.*, 2017; Degen *et al.*, 2018). Here we investigated the effect of pigment richness on all these key properties of ecological communities using a mechanistic community model describing light limited phytoplankton. We found that pigment richness increases species richness from one to two species on average (Fig. 5.2), has a unimodal effect on niche and fitness differences, and increases ecosystem function by about 60%.

5.5.1 Effects of pigment richness on species richness

Light has traditionally been considered as one resource until Stomp *et al.* (2004) showed that different wavelengths allow niche partitioning along the light spectrum, supporting coexistence. Our results confirm that this additional trait axis, representing pigmentation phenotypes, indeed allows introducing niche differences that allow coexistence of multiple species that would not have been possible if a single pigment would have been present (Stomp *et al.*, 2004, 2007a; Passarge *et al.*, 2006; Huisman & Weissing, 1994). However, our results also show that this mechanism alone cannot explain robust coexistence of many more species than two.

One important reason is the fact that pigments not only stimulate niche differences, but they also create competitive dominant and subordinate species, leading to large fitness differences, as they determine the total amount of absorbed photons ($\int_{400}^{700} k_p(\lambda) I_{in}(\lambda) d\lambda$). This result illustrates the effect of limiting similarity and the widespread occurrence of competitive exclusion despite trait differences (Meszéna *et al.*, 2006; Barabás *et al.*, 2012). While the light spectrum represents a continuous resource axis, along which an infinite number of species could specialise and persist, species that harvest too similar light colours will lead to the exclusion of the least fit. The fact that traits influence both niche and fitness differences has been pointed out for other traits in other systems as well (Mayfield & Levine, 2010). For example, Kraft *et al.* (2015) found that phenology of annual plants did not only promote niche differences but also inflated fitness differences. Gallego *et al.* (2019) found that a single trait, phytoplankton size, increases both niche and fitness differences. However, larger size differences between species does not promote coexistence.

Despite the extensive parameter range considered and the use of realistic pigmentation phenotypes, our analysis is a simplification of reality. In more complicated models, including additional factors, the effect of trait richness on species richness may be stronger. A first factor is individual-specific pigmentation. That is, the absorption spectrum of the same pigment may be different in different individuals from the same species, representing subtle but potentially important sources of inter- and intraspecific variation (Bricaud *et al.*, 2004; Six *et al.*, 2007; Bricaud *et al.*, 1995). Intraspecific variation of resource uptake traits can promote coexistence. For example, Hausch *et al.* (2018) recently showed that moderate intraspecific variation of bean weevils feeding on lentils and adzuki increased the resistance against invasion and invasion ability, thus promoting stable coexistence. However, theoretical results on annual plants obtained by Hart *et al.* (2016) suggest that initial intraspecific trait variation may also hamper coexistence. A second factor embodies trade-offs among traits. For example, species with less competitive pigmentation could have higher photosynthetic efficiencies, similar to larger phytoplankton species often having higher maximum growth rates (Langdon, 1988; Edwards *et al.*, 2015; Lavallée & Pick, 2002). Our assumption that all trait combinations were equally probable is therefore clearly a simplification of reality. A third factor is photoinhibition, which could facilitate coexistence, as it could turn our linear response of growth to light intensity into a non-linear response (Huisman & Weissing, 1994; Gerla *et al.*, 2011; Stomp *et al.*, 2007a). This would introduce the potential for relative non-linearities, which can contribute to temporal niche differentiation in case of external light intensity fluctuations (Litchman & Klausmeier, 2001). Litchman and Klausmeier showed that relative non-linearities can sustain coexistence of light-limited phytoplankton communities (Litchman & Klausmeier, 2001). Another way in which light intensity fluctuations could affect coexistence is through storage effects (Chesson, 2003). However, only one of the three conditions required for the storage effects are met. Indeed, in our system, environmental conditions do covary with competition, however, the response of all species is similar to these covariances and population growth is additive in environment and competition. By including a dormant stage, which is not sensitive to environmental fluctuations, Tredennick *et al.* (2017) showed that the storage effect leads to coexistence in a simple resource competition model. Including different phytoplankton life stages could serve as dormant stages in this model as well, and possibly promote a positive effect of pigment richness on species richness through storage effects.

5.5.2 Implications for ecosystem function

Our model showed that pigment richness positively affected ecosystem function (Fig. 5.4). However, coexistence requirements often caused the exclusion of many species in communities with high initial trait richness. This led to levels of ecosystem function that are comparable to that of communities with lower initial trait richness in which all species persist. This mechanism reduces the positive effect of trait richness on ecosystem function. Therefore, our results show how the effects of trait richness on ecosystem function can be limited on time scales that are sufficiently long for community dynamics to emerge. We simulated our communities to equilibrium, yet research has shown that phytoplankton communities are not at equilibrium, it is therefore not clear how applicable our results are (KEYMER, 1983). The limited long-term positive effect of trait richness on ecosystem function we find is due to the selection effect. Our results show that higher initial trait richness increases the probability of having a highly productive species present in the community (Appendix D.4). At the same time, complementarity is small in light limited phytoplankton communities (Appendix D.4). Cadotte (2017) have found that complementarity was most prominent in species and trait-rich plant communities.

Positive effects of trait richness on species richness and ecosystem function have been found in many different study systems. For example, diversity of feeding traits in herbivorous marine amphipods increased coexistence (Best *et al.*, 2013), mouth size differences facilitated coexistence of two bacterivorous ciliates (Violle *et al.*, 2011), and phylogenetic diversity, species richness and average productivity were all found to correlate positively in savanna grasslands (Cadotte *et al.*, 2009).

However, many of these studies share two features that may lead to higher trait diversity effects on function than we report on here. First, these experiments often are too short to observe competitive exclusion, and so species can contribute to function before they go extinct. Our results also show that it can take many generations to observe competitive exclusion, over 200 generations in our system, which is longer than most-long term experiments. Similarly long times to competitive exclusion have been found for phytoplankton species competing for two limiting resources (Sakavara *et al.*, 2017). Second, available experimental studies often consider communities with relatively few species. Our results show that the trait richness effect on species richness and function is most pronounced when trait richness, and therefore species richness, is relatively low (between 2 and 7 pigments).

Effects of trait diversity on ecosystem function of grasslands have been found to intensify with time (Reich *et al.*, 2012). This temporal intensification has been explained by reciprocal feedbacks between community composition and environmental conditions such as on soil nitrogen availability (Reich *et al.*, 2012). Our results show that, in absence of such feedbacks and when given enough time, effects of biodiversity on ecosystem function can actually weaken with time. That is, packing a more diverse set of species into our model system, light-limited phytoplankton, caused benefits for ecosystem function that were short-lived. These findings highlight the need to account for coexistence requirements when estimating the long-term benefits of biodiversity for ecosystem function (De Laender *et al.*, 2016; Bannar-Martin *et al.*, 2018).

5.6 Acknowledgements

We thank J. Huisman for comments on earlier versions of this manuscript and on the collection of pigmentation data. We thank M.Striebel and S.Fietz for providing data. This research used resources of the Plateforme Technologique de Calcul Intensif (PTCI) located at the University of Namur (http://www.ptci.unamur.be), Belgium, which is supported by the FRS-FNRS under convention No 2.4520.11. The PTCI is member of the Consortium des Équipements de Calcul Intensif (CÉCI) (http://www.ceci-hpc.be). F.D.L. received support from grants of the University of Namur (FSR Impulsionnel 48454E1), and the Fund for Scientific Research, FNRS (PDR T.0048.16).

Chapter 6

Mapping the diversity of species interactions

6.1 Abstract

Modern coexistence theory (MCT) holds the potential to study species persistence across community types but is rarely applied beyond pairs of competing species belonging to a single trophic level. Here, we show three benefits of applying MCT in multispecies communities, using recently developed methods that map species according to their niche ($\mathcal{N}$) and fitness differences ($\mathcal{F}$). First, $\mathcal{N} - \mathcal{F}$ mapping introduces a novel categorization of species and communities according to the high-level processes at play: *frequency dependence* (negative or positive), *the occurrence of positive species interactions*, and whether persistence is *conditional on niche differences or on the presence of other species*. Therefore, these categories describe whether species persistence is conditional ($\mathcal{F}$) and dependent ($\mathcal{N}$) on species interactions. Second, $\mathcal{N} - \mathcal{F}$ mapping facilitates studying species persistence along environmental gradients that shift intrinsic growth rates (environmental filtering) and the strength and sign of their interactions (network rewiring). Third, $\mathcal{N} - \mathcal{F}$ mapping has the potential to foster synthesis across community types because it can accommodate co-occurrence of positive (mutualism), negative (antagonism, competition) and neutral interactions between species. We therefore argue that $\mathcal{N} - \mathcal{F}$ mapping can promote collaboration across sub-fields, as it highlights how disparate ecological communities are different instances of a common concept.

6.2 From listing to mapping species interactions

Ecological communities contain a variety of interaction types, including positive (mutualism), negative (antagonism, competition) and neutral (commensalism, amensalism) interactions. In terrestrial communities, for example, plants share mycorrhizae while competing for light and nutrients, herbivores eat leaves, pollinators visit flowers, and many insects parasitize other insects. Understanding how species can persist amongst this amalgam of trophic and non-trophic interactions is generally considered intractable so different community types are typically treated independently (but see Kéfi *et al.* (2016); Thébault & Fontaine (2010)). While specialization improves understanding of the details of specific ecosystem types, it does not necessarily lead to a broader, system-independent, understanding.

Modern coexistence theory (MCT) holds the potential to identify similarities and differences in how species persist among community types, regardless of their interaction type. The main objective of MCT is to study coexistence and, more generally, persistence. MCT has been applied to study eco-evolutionary dynamics (Hart *et al.*, 2019), global change effects, and macroecological problems (Grainger *et al.*, 2019b). Two key concepts in MCT are niche differences ($\mathcal{N}$) and fitness differences ($\mathcal{F}$) (see a brief historical overview of these two concepts in Box 1). Niche differences measure how much stronger intraspecific interactions are than interspecific interactions. High niche differences promote coexistence. Fitness differences measure differences in the intrinsic competitive strength. High values of fitness differences hamper coexistence. Traditionally, however, $\mathcal{N}$ and $\mathcal{F}$ are studied for only a small subset of community types with few species (Adler *et al.*, 2018b): species pairs competing for common resources ('competing species pairs', Figure 6.2 and Figure 6.3 C). Alternative interaction types, including positive interactions (e.g. facilitation or mutualism), are typically not considered (but see Bimler *et al.* (2018)) either because available methods do not allow doing so (Chu & Adler, 2015) or result in interpretational problems when applied beyond the classic case of competing species pairs (Spaak & De Laender, 2020).

We use recently developed methods (Box 2) to show that quantifying $\mathcal{N}$ and $\mathcal{F}$ beyond competing species pairs allows studying the determinants of species persistence in ways that transcend the specifics of the community type. These methods permit mapping species according to their $\mathcal{N}$ and $\mathcal{F}$, much like a regular map provides information on spatial location. One of the main advantages of this framework is that the $\mathcal{N} - \mathcal{F}$ map provides information about why species persist, regardless of their particular guild, trophic position, or the sign and size of its interactions with other community members. Importantly, the map shows how previous work including stabilizing mechanisms and priority effects (Chesson, 2000; Ke & Letten, 2018) can be cast into a more general framework of species persistence (Figure 6.2). In what follows, we identify three reasons why this $\mathcal{N} - \mathcal{F}$ map is a useful research avenue.

6.3 Mapping $\mathcal{N}$ and $\mathcal{F}$ to categorize species and community types

Mapping $\mathcal{N}$ and $\mathcal{F}$ reveals which high-level processes explain species persistence in a given community. We identify three such processes, including the well-studied process of *frequency dependence* (negative ($0 < \mathcal{N}$), zero ($\mathcal{N} = 0$), or positive ($\mathcal{N} < 0$)). We also describe two new high-level processes. These are *the occurrence of positive species interactions* $(\mathcal{N} > 1)$, and whether *persistence* is ($F > 0$) or is not ($F < 0$) *conditional on niche differences or on the presence of other species* ($F > 1$) (Box 2 and Figure 6.1). Thus, broadly speaking, the $\mathcal{N} - \mathcal{F}$ map reflects whether species persistence is conditional ($\mathcal{F}$) and dependent ($\mathcal{N}$) on species interactions Figure 6.1.

The $\mathcal{N} - \mathcal{F}$ map can help formalising terminology that has proven challenging to pinpoint, such as environmental filtering (Cadotte, 2017) or priority effects (Fukami *et al.*, 2016; Ke & Letten, 2018). For example, environmental filtering can be defined as cases where $\mathcal{F} > 1$: species cannot realise positive growth in a given environment, and their persistence hinges on sufficiently large positive effects of other species $(\mathcal{N} > 1)$. While communities driven by priority effects have been linked to communities driven by stochastic forces, the $\mathcal{N} - \mathcal{F}$ map shows that species from both types of communities will occupy different regions in the $\mathcal{N} - \mathcal{F}$ map. While $\mathcal{N} = \mathcal{F} = 0$ in communities purely driven by stochastic forces (i.e. neutrality), $\mathcal{N} < 0$ and $\mathcal{F} < 1$ in case of priority effects.

Mapping species from the same community on the $\mathcal{N} - \mathcal{F}$ map highlights the diversity of high-level processes that occur simultaneously and sustain species persistence in the given community. Three simple examples illustrate this categorization in different community types (Figure 6.3A). Priority effects (Figure 6.3A "priority effects") occur when species can grow when alone ($\mathcal{F} < 1$) but cannot persist in a community because they experience positive frequency dependence ($\mathcal{N} < 0$) (Mordecai, 2011; Fukami *et al.*, 2016; Ke & Letten, 2018). For non-obligatory mutualism (Figure 6.3A "mutualism"), the map formalizes the idea that species persist because of positive interactions $(\mathcal{N} > 1)$, but also that this persistence is not *conditional* on the presence of other species (i.e. $\mathcal{F} < 1$), i.e. species realise positive growth when grown alone and do not *need* the presence of other community members. In case of asym-

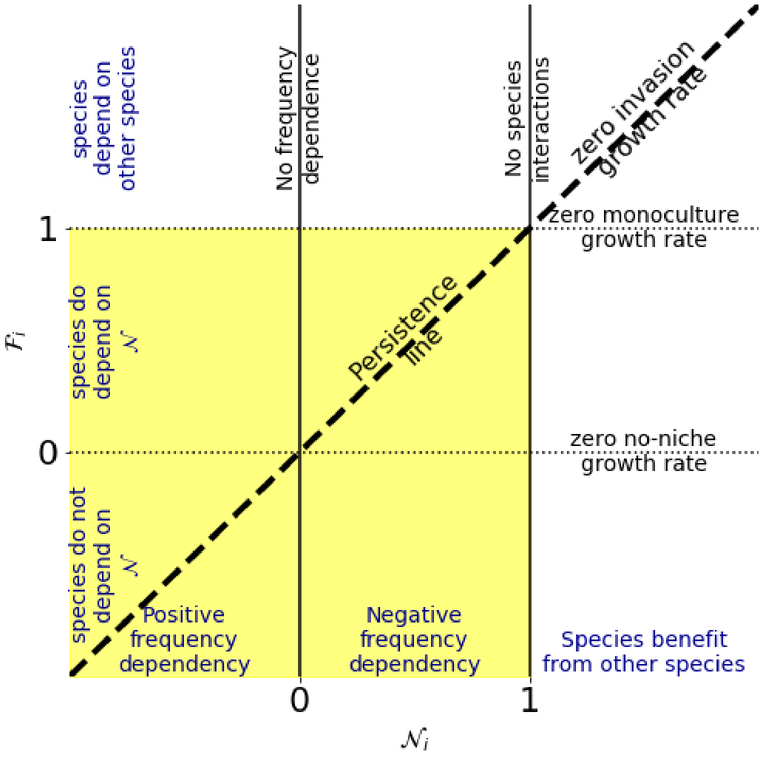

Figure 6.1: Niche and fitness differences allow positioning each species in the niche and fitness differences map ($\mathcal{N} - \mathcal{F}$ map). The map extends in all four directions to infinity and is divided into different regions by five lines (black text). The diagonal line is the persistence line ($\mathcal{N} = \mathcal{F}$), below which species are assumed to persist ($\mathcal{N} > \mathcal{F}$), and above which species may go extinct ($\mathcal{N} < \mathcal{F}$). The other four lines divide both niche and fitness differences into three qualitative different sections each (blue text), leading to a total of nine different regions in the $\mathcal{N} - \mathcal{F}$ map (See Box 2 for specific details).

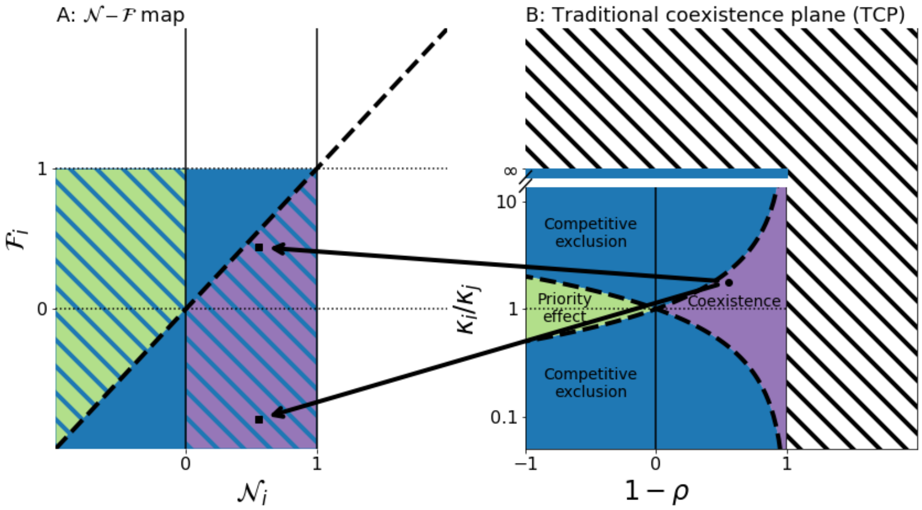

Figure 6.2: The - map (A) differs from the traditional coexistence plane (TCP, B, adapted from Ke & Letten (2018)). First, the TCP describes communities (black dot), while the - map locates species (black squares). The two squares (A) correspond to the two species from the black-dot-community (B). Thus, the - map can map all processes driving the persistence of each individual species. Second, regions in TCP consequently label community properties such as priority effects (green), competitive exclusion (blue) and coexistence (purple). Instead, regions in the - map label species properties (e.g. positive frequency dependence). Importantly, community properties do not automatically imply certain species properties and vice-versa. For example, a species from a community with priority effects could be located anywhere in the green-blue hatched region. Likewise, a species from a community in which competitive exclusion occurs can be located in both the blue and blue hatched regions. Note, however, that these colours illustrate competitive two species communities. For other community types, other colour codes will apply. Third, TCP cannot analyse communities with facilitation ($\mathcal{N} > 1$) or species with negative intrinsic growth rates ($\mathcal{F} > \infty$), as indicated by the black-white hatched region. Instead, - mapping will locate species with such properties in the white region.

metric species interactions such as ”competition-facilitation” or prey-predator communities (Figure 6.3A ”competition-facilitation”), negative frequency dependence and positive interactions co-occur. When applied to more complex communities, categorization can lead to increasingly new insights about which processes underpin persistence. For example, in the simple six species food-web example (Figure 6.3B), the categorization reveals that (1) one basal species (e.g. a primary producer) can persist without any niche differentiation, while the other two cannot, and (2) that primary consumers and predators need positive species interactions to persist. In contrast to the examples from Figure 6.3A, these results (i.e. the prevalence of specific high-level processes) cannot be gauged directly from the community interaction matrix and need a formal treatment via $\mathcal{N}$ and $\mathcal{F}$ computations in order to be informative (Box 1).

The $\mathcal{N} - \mathcal{F}$ map can help connecting coexistence theory to ecological network theory across different community types (Godoy *et al.*, 2018). So far, MCT focused primarily on simple two species communities, i.e. without indirect and higher order interactions (Chesson, 2000; Godoy & Levine, 2014; Grainger *et al.*, 2019a; Levine & HilleRisLambers, 2009; Narwani *et al.*, 2013) but see (Godoy *et al.*, 2018, 2017; Petry *et al.*, 2018). The $\mathcal{N} - \mathcal{F}$ map is based on multispecies-equilibria and therefore accounts for the non-trivial effects of indirect and high order interactions on persistence, arising in highly diverse communities (Grilli *et al.*, 2017; Saavedra *et al.*, 2017; Spaak & De Laender, 2020). Thus, $\mathcal{N} - \mathcal{F}$ mapping can connect these two fields.

Although the $\mathcal{N} - \mathcal{F}$ map addresses the complexity of ecological networks, it also provides information on which processes determine the persistence or exclusion of specific species and trophic guilds. Previous approaches on ecological networks are based on the stability of the Jacobian matrix at equilibrium (Allesina & Tang, 2015; Levine *et al.*, 2017). They can very efficiently analyse complex communities but give little to no insight into which species will go extinct in an unstable community. Conversely, $\mathcal{N}$ and $\mathcal{F}$ are defined at the species level with respect to the rest of the community members and therefore integrate both species and community levels responses to ecological interactions.

Box 1: Defining niche and fitness differences Niche differences have been originally described for pairs of species competing for shared resources. As such, niche differences ($1-\rho$), the opposite of niche overlap (ρ), have been conceptualised as the dissimilarity of the consumption vectors of two species (Chesson, 1990; Hurlbert, 1978). Niche differences of 0 meant the consumption vectors are identical, while niche differences of 1 meant the species do not consume common resources. In between cases meant species limit themselves more than they limit others, i.e. interspecific interactions are less negative than intraspecific interactions (Adler *et al.*, 2007). Consequently, negative niche differences were interpreted as weaker intraspecific interactions than interspecific interactions, which corresponds to positive frequency dependence (Fukami *et al.*, 2016; Ke & Letten, 2018; Mordecai, 2011). Apart from niche differences, also fitness differences are needed to assess the outcome of species interactions (Chesson, 2000). Fitness differences measure the difference in inherent competitive strength between both species if niche differences would be absent (Adler *et al.*, 2007). For two competitors to coexist, niche differences must overcome fitness differences. If both species perform equally well, the fitness differences of both species are 0 (other definitions chose 1 for equal performance (Adler *et al.*, 2007; Carroll *et al.*, 2011; Chesson, 2013; Godoy & Levine, 2014). Recent developments in MCT have led to three main insights. First, while niche and fitness differences have been traditionally considered community properties (above text and Figure 6.2B), this is only true for the specific case of competing species pairs. In virtually all other community types, niche and fitness differences must be species properties (Adler *et al.*, 2007; Spaak & De Laender, 2020). Second, niche differences can exceed 1, where they indicate positive interspecific interactions, e.g. facilitation or predation (Figure 6.3A and B) (Spaak & De Laender, 2020). Third, species with negative intrinsic growth rates have higher fitness differences (lower fitness) than species with zero intrinsic growth rate, e.g. obligatory mutualists or predators (Figure 6.4A and B). Fitness differences exceeding 1 indicate negative intrinsic growth rate.

Box 2: How niche and fitness differences reveal high level processes
We first define $\mathcal{N}_i$ and $\mathcal{F}_i$ mathematically for a community in which the per-capita growth rate of species i, f_i, depends on species i's density X_i and that of the other species (contained in the vector $X^{(-i)}$): $\frac{1}{X_i}\frac{dX_i}{dt} = f_i\left(X_i, X^{(-i)}\right)$. For such a community we define the species-specific $\mathcal{N}_i$ and $\mathcal{F}_i$ as:

$$\mathcal{N}_i = \frac{f_i\left(0, X^{(-i,*)}\right) - f_i\left(\sum_j c_{ij}X_j^{(-i,*)}, 0\right)}{f_i(0,0) - f_i\left(\sum_j c_{ij}X_j^{(-i,*)}, 0\right)} \tag{6.1}$$

$$\mathcal{F}_i = \frac{-f_i\left(\sum_j c_{ij}X_j^{(-i,*)}, 0\right)}{f_i(0,0) - f_i\left(\sum_j c_{ij}X_j^{(-i,*)}, 0\right)} \tag{6.2}$$

Where $f_i\left(0, X^{(-i,*)}\right)$ is the invasion growth rate, $f_i\left(\sum_j c_{ij}X_j^{(-i,*)}, 0\right)$ is the no-niche growth rate, $f_i(0,0)$ is the intrinsic growth rate, $X_j^{(-i,*)}$ is the equilibrium density of species j in the resident community, and c_{ij} is a conversion factor that ensures equal total dependence on limiting factors. Note that these definitions differ slightly from the original ones (Spaak & De Laender, 2020) to facilitate visualisation on the $\mathcal{N} - \mathcal{F}$ map. These equations may be daunting to look at and not straight forward to solve analytically. For this we have created computer code than can automatically compute $\mathcal{N}_i$ and $\mathcal{F}_i$ as well as the conversion factors c_{ij}. This computer code runs on both R and python:
https://github.com/juergspaak/NFD_definitions. These definitions show that (1) $\mathcal{N}$ measures frequency dependence, while $\mathcal{F}$ measures competitive strength, (2) the three growth rates carry the following biological interpretation: The invasion growth rate quantifies if species can persist (positive invasion growth rates, $\mathcal{N}_i > \mathcal{F}_i$), or not (negative invasion growth rates, $\mathcal{N}_i < \mathcal{F}_i$). The persistence line (Figure 6.2) separates these two cases. The intrinsic growth rate measures growth in absence of other species and thus tells which species survive in monoculture ($\mathcal{F}_i < 1$), e.g. basal species relying on abiotic resources. Species with negative intrinsic growth rates ($\mathcal{F}_i > 1$) depend on other species to persist; e.g. herbivores and predators. The no-niche growth rate measures growth in the absence of niche differences. Species with positive no-niche growth rates ($\mathcal{F}_i < 0$) persist in the absence of niche differences. Species with negative no-niche growth rates

($\mathcal{F}_i > 0$) persist only when niche differences are sufficiently large. Comparing these growth rates to each other gives further insight. For example, species with invasion growth rates smaller than no-niche growth rates exhibit positive frequency dependence ($\mathcal{N}_i < 0$), e.g. because of priority effects (Ke & Letten, 2018). Conversely, species with negative frequency dependence ($\mathcal{N}_i > 0$), grow faster when rare. Finally, species with an invasion growth rate that exceeds their intrinsic growth rate ($\mathcal{N}_i > 1$) grow faster in a community than when alone. Examples include predators and mutualists.

6.4 Mapping $\mathcal{N}$ and $\mathcal{F}$ to understand environmental change effects on persistence

One important aim in ecology is to understand how changes in environmental conditions affect the ability of species to persist. We know that environmental change can affect species persistence, but to mitigate its effects we must move from a qualitative understanding to a quantitative measure of persistence.

MCT posits that persistence of a species depends on how well adapted a species is to its environment compared to other species ($\mathcal{F}$) and how species differences buffer or aggravate the (dis-)advantage a species has because of its adaptedness ($\mathcal{N}$). The $\mathcal{N} - \mathcal{F}$ map allows to disentangle the effects of environmental change into the same categories. For example, pH increases niche differences, but not fitness differences in yeast cultures (Grainger *et al.*, 2019a). Additionally, the $\mathcal{N} - \mathcal{F}$ map gives not only qualitative information about persistence (yes or no), but also quantitative (how close is a species to the persistence line?). Species that are on the brim of extinction due to environmental change will be located closer to the persistence line than other species.

Similarly, prior work has systematically shown that the sign, strength, and presence (Valiente-Banuet *et al.*, 2015) of species interactions change along broad environmental gradients (e.g. nutrient enrichment (Harpole & Tilman, 2007), warming (Traill *et al.*, 2010), drought (Bimler *et al.*, 2018), or environmental pollution (Baert *et al.*, 2016). However, connecting shifts of species interactions with persistence has only recently started (Cenci & Saavedra, 2018), for example using species pairs of yeast (Grainger *et al.*, 2019a) and annual plants (Bimler *et al.*, 2018; Lanuza *et al.*, 2018). The proposed framework can facilitate such studies as it maps how changes in multispecies interactions relate to the aforementioned high-level processes. The framework is therefore well-suited to understand how environmental change will affect the persistence of which species and why. To illustrate this point, we provide two examples with simple

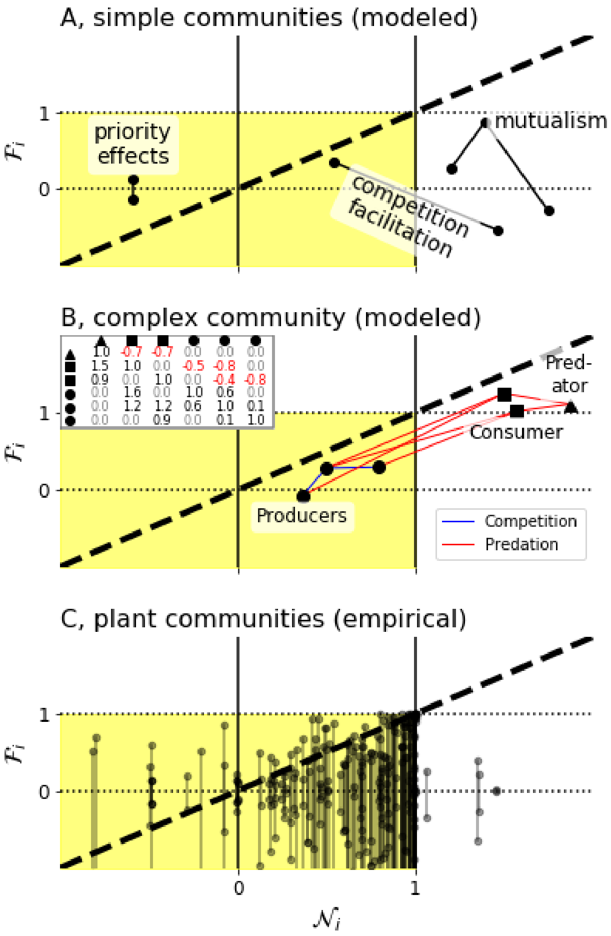

Figure 6.3: $\mathcal{N}-\mathcal{F}$ mapping allows the analysis of species persistence across a variety of community types using a single framework. The black lines and yellow area are those of Figure 6.1. A: Three examples of simple communities with different kinds of species interactions. Dots represent species, connections represent direct interactions. All three communities follow Lotka-Volterra dynamics ($\frac{1}{N}\frac{dN}{dt} = \mu - AN$) with $\mu = 1$ but different interaction matrices to represent different interaction types: priority effects $\begin{pmatrix} 1 & 1.2 \\ 2.0 & 1 \end{pmatrix}$, competition-facilitation $\begin{pmatrix} 1 & 0.7 \\ -0.3 & 1 \end{pmatrix}$, and mutualism $\begin{pmatrix} 1 & -0.2 & 0 \\ -0.2 & 1 & -0.4 \\ 0 & -1.6 & 1 \end{pmatrix}$. B: An example of a food web containing three producers (dots), two consumers (squares) and one predator (triangle); Connections are direct interactions. Importantly, the position of each species depends on all its direct *and* indirect interactions with other species. The interaction matrix is shown in the inset. The intrinsic growth rates are $\mu = (-2, -10, -1, 38, 50, 32)$ (species are ordered as in the interaction matrix). C: $\mathcal{N}-\mathcal{F}$ mapping of 169 empirical plant communities, taken from a recent review (Adler *et al.*, 2018b), with dots and connections as in the other panels. We converted the original $\mathcal{N}$ and $\mathcal{F}$ from (Adler *et al.*, 2018b) to the definition by (Spaak & De Laender, 2020) (see Box 2). This panel shows that most studies have experimentally investigated communities with $\mathcal{N} < 1$ and $\mathcal{F} < 1$; there has been some exploration of communities under positive frequency dependence ($\mathcal{N} < 0$) but there is virtually no exploration of ecological communities with $\mathcal{F} > 1$ in MCT, but see (Petry *et al.*, 2018), suggesting that persistence in many community types that present positive interactions has remained unexplored.

(Figure 6.4A) and more complex communities (Figure 6.4B). For illustration, we assume that environmental change causes an absolute increase in species interactions, and a decrease in intrinsic growth rate. This reflects environmental change depressing growth and making negative interactions less negative (i.e. weaker), and potentially even positive when the change is large enough, i.e. corresponding to a prevailing argument in community ecology (Maestre *et al.*, 2012; De Laender *et al.*, 2016). This illustration shows that weakening, and potentially even sign-switching, of species interactions can qualitatively change the location of species within the $\mathcal{N}-\mathcal{F}$ map (Figure 6.4A& B). For example, environmental change transforms priority effects (Figure 6.3A ″priority effects″) into the classic case of resource competition (Figure 6.4A ″resource competition″), where species persist when negative frequency dependence ($0<\mathcal{N}<1$) is strong enough to overcome differences in competitive ability ($\mathcal{F}<1$). Likewise, environmental change transforms ″facilitation-competition″ (Figure 6.3A) into ″mutualism″ (Figure 6.4A) because environmental change makes species interactions both positive and therefore symmetric in sign. Finally, in a mutualistic community (Figure 6.3A, ″mutualism″), environmental change makes the persistence of one species conditional on the presence of the other community members (Figure 6.4A, ″obligatory mutualism″). Environmental change has depressed the intrinsic growth rate of this species so much as to make it negative, such that it cannot realise positive growth when present alone (and thus has $\mathcal{F}>1$). Finally, an environmental change driver affecting consumers (Figure 6.3B) will lead to indirect effects on the mapping of the other trophic levels (Figure 6.4B). Prior to environmental change, the persistence of the species with minimal $\mathcal{F}$ does not depend on niche differences. Environmental change increases $\mathcal{F}$ of this species above zero, making the persistence of all species dependent on niche differences.

Taken together, these illustrations highlight that the $\mathcal{N}-\mathcal{F}$ map allows understanding species persistence along environmental gradients. While $\mathcal{N}$ and $\mathcal{F}$ are species-specific (Adler *et al.*, 2007; Spaak & De Laender, 2020), the map also provides community-level information because all $\mathcal{N}$ and $\mathcal{F}$ depend on the $\mathcal{N}$ and $\mathcal{F}$ of the other community members and the environmental effects thereon. The consideration of both scales unlocks opportunities to ask which community members will be the first to have their persistence altered once an environmental change sets in, and how environmental change affects the general distribution of species.

6.5 Mapping $\mathcal{N}$ and $\mathcal{F}$ to foster synthesis in community ecology

Synthesis is a key task in community ecology, a discipline where a variety of models, hypotheses, and theories aim at understanding a variety of interaction types, haunted by the idea that specificities outnumber generalities (Lawton, 1999). However, the way to pursue this synthesis is not straightforward. Much progress has been made conceptually, by summarizing the main processes driving community assembly and composition (Vellend, 2016). However, quantitative approaches that allow pinpointing similarities and differences among disparate community types, arguably one of the first steps towards across-system synthesis, are less common. Quantitative syntheses should rely on common computational frameworks applied to disparate data (Carpenter *et al.*, 2009; Poisot *et al.*, 2019). Yet, most available approaches rely on indirect comparisons, i.e. they examine to what extent models match data collected in different communities (Etienne *et al.*, 2019; Rip & Mccann, 2011). The $\mathcal{N} - \mathcal{F}$ map can contribute to synthesis because it represents a direct approach to community comparison (however, see 'limitations') which allows syntheses that were not available before. Specifically, the $\mathcal{N} - \mathcal{F}$ map provides common currency across ecological disciplines (Grainger *et al.*, 2019b), which makes it possible to ask a suite of novel questions. One example is whether species persistence in communities that harbour distinct interaction types (e.g. plant-pollinator networks versus food webs) is driven by the same high-level processes or not. Another question deals with the evolution of species interactions, asking if phylogeny or evolutionary-constrained traits (e.g. size, feeding role) predict $\mathcal{N} - \mathcal{F}$ mapping across contrasting taxonomic groups (e.g. plants, plankton, and vertebrates) (Gallego *et al.*, 2019; Pérez-Ramos *et al.*, 2019). Addressing such questions will facilitate across-community comparisons, which allows examining how the complexity of interaction types and ecological network architecture affect the dynamics of ecological communities and their maintenance.

6.6 Limitations

Assessing persistence directly is challenging (Clark *et al.*, 2019b; Huisman & Weissing, 1999; Schreiber, 2017, 2000). MCT has traditionally assessed persistence through "invasion analysis" , which tests whether all species in a community are able to increase in abundance when rare (Chesson, 2000, 1994; Ellner *et al.*, 2019). $\mathcal{N} - \mathcal{F}$ mapping does not alter how we asses persistence, and

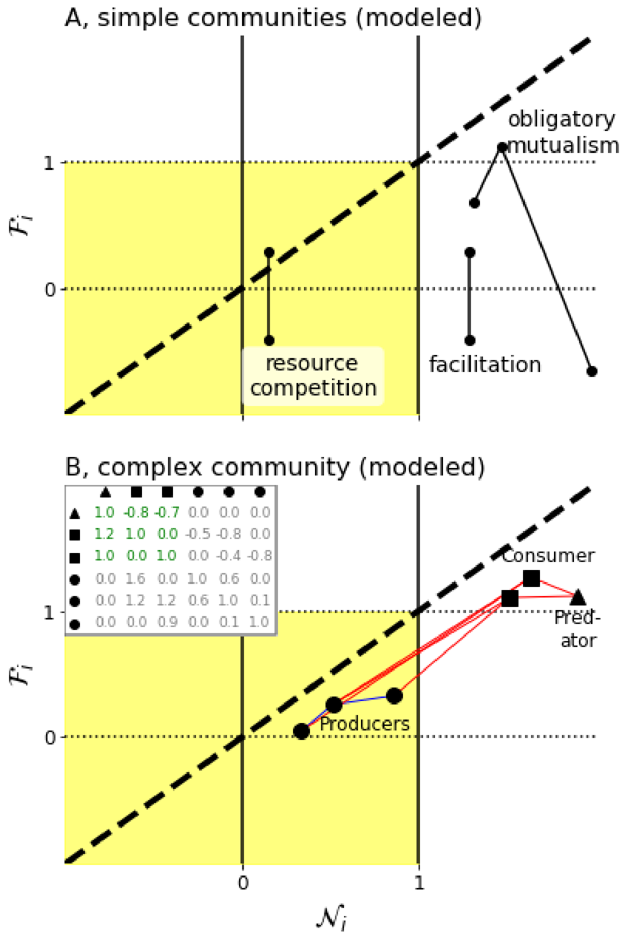

Figure 6.4: $\mathcal{N}-\mathcal{F}$ mapping can help understanding the effects of environmental change on persistence. A: The communities from Figure 6.3A were exposed to an environmental change driver that decreases the interspecific interactions strength and reduces the intrinsic growth rates. These effects shift priority effects to resource competition, competition-facilitation to mutualism, and creates one obligate mutualist. The new interaction matrices are: resource competition: $\begin{pmatrix} 1 & 0.6 \\ 1.2 & 1 \end{pmatrix}$, mutualism $\begin{pmatrix} 1 & -0.4 \\ -0.2 & 1 \end{pmatrix}$, obligatory mutualism $\begin{pmatrix} 1 & -0.2 & 0 \\ -0.5 & 1 & -0.6 \\ 0 & -1.6 & 1 \end{pmatrix}$. The new intrinsic growth rates are $\mu = 0.8$, expect for the obligatory mutualism community, in which it is $\mu = (0.8, -0.2, 0.6)$ B: The communities from Figure 6.3B were exposed to an environmental change driver that reduces interactions among consumer species (interaction matrix in the top-left; interaction strengths among consumers are in green) as well as the intrinsic growth rate of consumers $\mu = (-2, -10, -5, 38, 50, 25)$. Note that these direct effects change the $\mathcal{N}-\mathcal{F}$ mapping of the other species as well via indirect (top-down) effects.

it therefore inherits all the limitations of invasion analysis. These limitations include the fact that the requirement of a positive invasion growth rate is a too stringent criterion for persistence, and that in some community types invasion analysis is technically impossible(Barabás *et al.*, 2018; Grilli *et al.*, 2017; Pande *et al.*, 2019; Saavedra *et al.*, 2017).

In communities where invasion analysis is both possible and useful, a second limitation may emerge. That is, measuring $\mathcal{N}$ and $\mathcal{F}$ can be labour-intensive, especially in species-rich communities. One option is to empirically measure different kinds of growth rates (see Box 2 for the three growth rates that define $\mathcal{N}$ and $\mathcal{F}$ as quantified here, (Spaak & De Laender, 2020)). Alternatively, one can parameterize a community model (Baert *et al.*, 2016; Carrara *et al.*, 2015; Maynard *et al.*, 2019) and derive $\mathcal{N}$ and $\mathcal{F}$ either analytically or through simulations. Both approaches (empirically measuring growth rates and parameterizing models) are potentially labour-demanding and various trade-offs emerge regarding the model complexity that is appropriate to represent the system considered (Clark *et al.*, 2019a).

6.7 Conclusions

We propose a framework that extends modern coexistence theory (MCT) towards a variety of species interactions. This framework is based on redefining niche and fitness differences as species-specific characteristics that yield information about which high-level processes underpin persistence (Box 2). In this way, the approach summarizes the effect that many species interactions can have on persistence, regardless of species- or community-specifics. This common framework represents an unprecedented opportunity to examine how multiple interaction types in various ecological networks contribute to the maintenance of biodiversity. Because it accommodates multiple interaction types, the framework can inspect how environmental factors, both via direct and indirect effects, affect persistence of which species, both positively and negatively.

The $\mathcal{N}-\mathcal{F}$ map connects to both the history and the future of MCT. It includes previously described regions of the theory (competing species pairs, Figure 6.2B), but uncovers new regions that represent other interaction types, yielding insights previously unknown (Figure 6.2A). Which kind of communities fit under these previously unexplored regions is a new research field awaiting exploration. We believe this uncovering can trigger collaboration between different sub-disciplines in ecology, most notably among different groups of empiricists. Different interaction types may lead to similar $\mathcal{N}-\mathcal{F}$ mapping, showing that - despite these differences - the same high-level processes drive persistence. Finally, we believe that formalising species interactions with the $\mathcal{N} - \mathcal{F}$ map will also foster collaboration between theoreticians and empiricists because mapping can be based on models and empirically measured growth rates. Overall, our framework illustrates how simple definitions of species interactions create a reference system that rules all species interaction types and communities.

Chapter 7

Discussion

7.1 A synthesis of my thesis

7.1.1 How community types affect niche and fitness differences

Chapters 2 to 6 all use very different community types and models. Comparing their results therefore yields insight in how they affect niche and fitness differences (see below). However, I want to stress that the chapters do not only differ in the aspect specifically mentioned in figure 7.1, nor have the chapters been designed in advance to test these aspects. Rather, in retrospect, we see these differences and can investigate whether it is probable that a certain aspect is responsible for the differences between their niche and fitness differences.

Such a comparison is legitimate, because I applied the same definition of niche and fitness differences in all the different chapters. I will use the formula for fitness differences used in chapter 6 throughout the discussion. This consistency of niche and fitness differences is an important step forward, because so far, the niche and fitness differences definition and community models were clustered. For example, annual plant models were almost exclusively analysed with the definition of Godoy & Levine (2014), whereas phytoplankton communities were almost exclusively analysed with the definition of Carroll *et al.* (2011). As a result, we could not easily compare the results of, say, Narwani *et al.* (2013), who found relatively small niche differences in phytoplankton to, say, Germain *et al.* (2016), who found relatively large niche differences in terrestrial plants. We do not know whether the different averages of niche differences are based on differences in the biological systems or merely due to the definition they used.

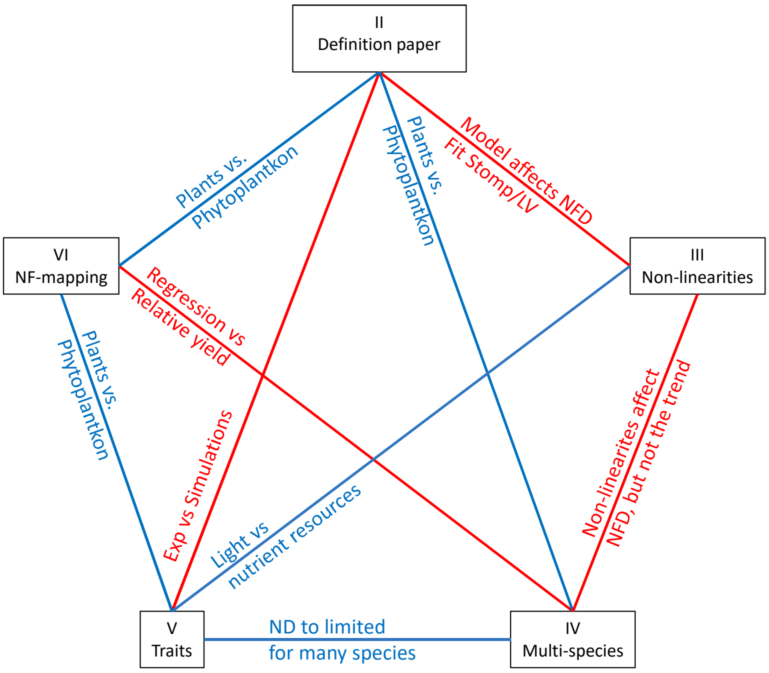

Figure 7.1: I used different community types or models in different chapters. Comparing two chapters with different community types may give insight how community types affect niche and fitness differences (blue lines, section 7.1.1). Additionally, some chapters use the same or similar community types, but different community models. Comparing these may give insight how community models affect niche and fitness differences (red lines, section 7.1.2). Importantly, we expect community types to affect niche and fitness differences, as the underlying biology is different. However, the community model should *not* affect niche and fitness differences (assuming the model matches the empirical data), as the underlying biology is the same. Yet, as I show in section 7.1.2, the choice of a community model can have large effects on niche and fitness differences.

Phytoplankton communities have lower niche differences than terrestrial plants

Chapter 2 and 5 both investigate niche and fitness differences in phytoplankton communities, while the literature data from chapter 3 and 6 are mainly from terrestrial plants. Terrestrial plants tend to have, on average, higher niche and fitness differences than phytoplankton species (Figures 4.4 and 6.3C versus Figure 5.3). The variation of niche and fitness differences is also much higher in terrestrial plants, however, this may be primarily because of larger sample sizes for terrestrial plants, so I will not investigate this further. Both Venail *et al.* (2014) and Narwani *et al.* (2013) found comparatively small niche and fitness differences for phytoplankton. On the other hand, Germain *et al.* (2016) and Godoy & Levine (2014) found strong niche and fitness differences for annual plants.

The differences found in my PhD thesis as well as in these literature data may report a real phenomenon. We know that phytoplankton communities are relatively simple and offer little possibilities for niche differentiation (Hutchinson, 1959). On the other hand, Kraft *et al.* (2015) showed that niche differences in annual plants depend on many functional traits, implying that competition in annual plants offers many possibilities for niche differentiation.

But just as well, the differences may be due to some other non-investigated fact. For example, both studies on phytoplankton were communities in microcosm short term experiments using the definition of Carroll *et al.* (2011). Both studies on terrestrial plants were mid-long term field studies using the definition of Godoy & Levine (2014). I showed in chapter 2 that different definitions applied to the same community yields different niche and fitness differences. Additionally, Adler *et al.* (2018b) showed that LV models fitted to experiments tend to have lower niche differences than LV models fitted to field data.

The empirical and theoretical data confirm the a priori expectations that terrestrial plants should have higher niche differences than phytoplankton communities, however, I do not think that they provide sufficient evidence to conclude this. A similar hypothesis could be tested to investigate whether other communities tend to have even higher niche and fitness differences.

Competition for light wavelength contributes comparatively little to niche differences in phytoplankton communities

Chapter 2 and 5 both investigate niche and fitness differences in phytoplankton, once for light-limited and once for nutrient-limited phytoplankton. To compare the results, I generated phytoplankton species with resource uptake and consumption traits according to the literature (Edwards & Stachowicz, 2012), see E.2.

In all simulations, competition for light leads to relatively small niche and fitness differences (Fig. 7.2, blue dots). Some of the communities coexisted (35%) and in some communities one species excluded the other (65%). However, these specific percentages may very likely depend on the specific model parameters, such as incoming light intensity or dilution rate. None of the communities were governed by priority effects.

Competition for essential resources leads to a high variation of niche and fitness differences coupled with more diverse outcomes of species interactions (Fig. 7.2, red dots). All outcomes of species interactions were present, where the clear majority was competitive exclusion (89%). Coexistence (6%) and priority effects (5%) were approximately equally likely, but again, the specific numbers may depend on the specific parameter settings. Additionally, in most communities (60%), niche differences were completely absent as both species were limited by the same resources.

An obvious question is which of these processes contributes more to natural phytoplankton diversity. However, the available data is not sufficient to answer this question. Competition for different light wavelength only leads to small niche and fitness differences, that is, coexistence may be relatively unstable, but can allow up to four species coexist (Chapter 5). Conversely, competition for limited resources can allow for strong niche and fitness differences, i.e. very stable coexistence, but allow only as many species to coexist as there are limiting resources, in this case two (Tilman, 1982). To answer this question, one would have to include competition for resources and light into one model and investigate how species richness depends on both mechanisms.

Niche and fitness differences in multispecies communities

Chapter 4 and 5 both investigate niche and fitness differences in multispecies communities, once species richness is an independent variable and once it is a dependent variable. The results from chapter 4 can, to some extent, explain the results from chapter 5. Niche differences in light-limited phytoplankton communities with two species are very limited. Species can coexist because their fitness differences are also very small. However, increasing species richness will increase fitness differences. These will be too strong for the small niche differences and, as a result, species will not coexist.

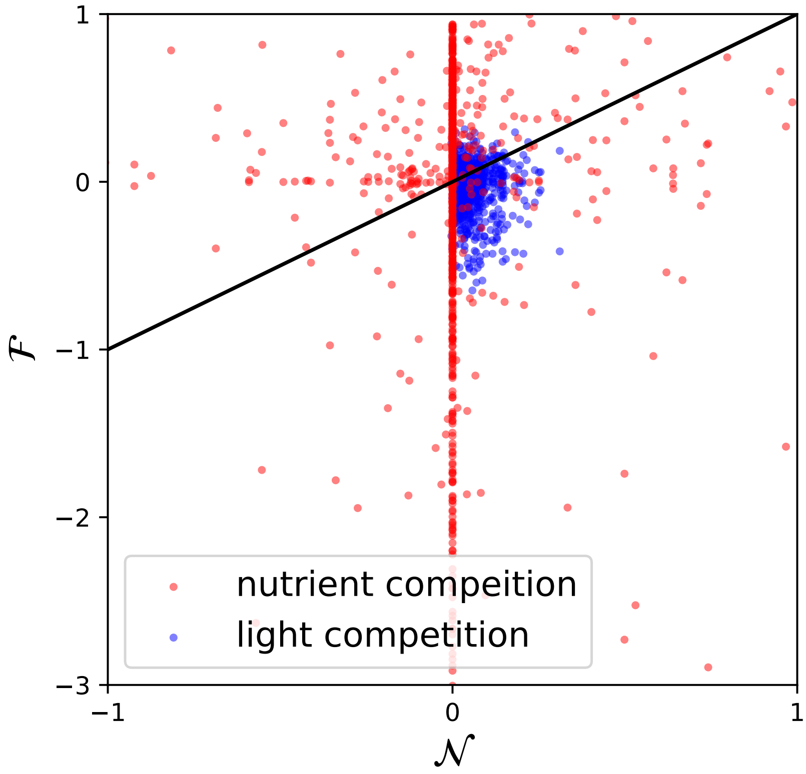

Figure 7.2: Competition for light wavelength leads to relatively small niche and fitness differences (blue). Conversely, competition for essential resources can lead to both strong negative and strong positive niche differences (red). Competition for limiting resources leads to all three possible outcomes of competition (coexistence, competitive exclusion and priority effects). In many communities both species were limited by the same resources, which led to the absence of niche differences.

7.1.2 How community models affect niche and fitness differences

During my PhD, I investigated several different community models including phenomenological (LV models with higher-order interactions) and mechanistic (Tilman's resource competition models and the Stomp model for light competition). Chapter 3 specifically dealt with how the model choice and model approximation may affect niche and fitness differences. However, chapter 3 was predominantly qualitative, but here, I want to explore this issue more quantitatively.

Community models lead to smaller niche and fitness differences than experiments

Chapter 2 and 5 both investigate niche and fitness differences in light-limited phytoplankton communities, once in an experimental setting and once in simulations. Niche and fitness differences observed in the experimental setting were much larger than the niche and fitness differences from the numerical simulations (Fig. 7.3).

The experimental measurements of niche and fitness differences from chapter 2 were performed with two cyanobacteria species with relatively low dilution rates compared to the dilution rates from chapter 5. To compare the results to the simulated niche and fitness differences from chapter 5, I computed niche and fitness differences for the Stomp model with three varying assumptions. First, I measured the absorption spectra of the cyanobacteria (E.3) and fitted the Stomp model to obtain the photosynthetic efficiency ϕ (green dots). However, the Stomp model did not fit the data perfectly ($R^2 \approx 0.82$, E.3). Importantly the fitted Stomp model did not correctly predict coexistence of the two species. Second, I used the empirically measured absorption spectra and used similar photosynthetic efficiencies as in chapter 5 (blue dots). Third, I generated the absorption spectra of cyanobacteria species belonging to the pigmentation types used in the experiment (red dots). This approach is most comparable to the phytoplankton communities in chapter 5. However, both niche and fitness differences are considerably larger than in chapter 5 (Figure 5.3), because we only focus on two pigmentation types that have very dissimilar absorption spectra.

The experimentally measured niche differences (purple dots) are much larger than the ones obtained with the Stomp model, regardless of the specificities chosen for the Stomp model. This implies that the Stomp model does not capture all mechanisms for niche differentiation. Similarly, Chu & Adler (2015) fitted a community model to the long-term field data of perennial plants in order to compute niche and fitness differences. Later Adler *et al.* (2018a) showed that this model gives poor predictions of how the community will respond to artificially removing species from the community, that is, the community model underestimated competitive release.

I was not able to accurately fit the Stomp model to the empirical data from chapter 2. During my PhD, I performed a total of 5 experiments with a total of 180 experimental units with varying experimental procedures, and in none of them did the Stomp model explains more than 85% of the variance of the community densities. However, my experimental setup differed in several ways from the original setup used in Stomp *et al.* (2004). First, Stomp *et al.* (2004) used chemostats, while I used semi-continuous batch cultures with volumes ranging from 5 to 500 ml. Importantly, debris may accumulate in these semi-continuous batch cultures. Second, Stomp *et al.* (2004) was run at much higher dilution rates of $0.014h^{-1}$, where my dilution rates ranged from $0.0006h^{-1}$ to $0.0026h^{-1}$.

Do higher order interactions affect niche and fitness differences?

Chapter 3 and 4 both investigate how higher order interactions affect niche and fitness differences. Initially, their findings seem to contradict each other, as in chapter 4 I found that higher order interactions do not affect niche differences, while in chapter 3 they do.

However, chapter 4 focuses on how species richness affects niche and fitness differences on average. Higher order interactions do not affect this trend, nor do communities with higher order interactions have higher or lower niche differences on average. Finally, in chapter 3, I assumed that all higher order interactions coefficients are equally strong on average.

Higher order interactions affect niche and fitness differences just as we would expect them given their effect on first-order interactions. β_{iii} and β_{jjj} increase the first-order intraspecific interactions (α_{ii} and α_{jj}), which therefore increases $\mathcal{N}_i$ (Fig. 7.4 A, yellow and purple lines). β_{ijj} and β_{jii} increase the first-order interspecific interactions (α_{ij} and α_{ji}) and therefore decreases $\mathcal{N}_i$ (Fig. 7.4 A, cyan and orange lines). The other higher order interactions do not affect the monoculture growth rates nor the invasion growth rates, therefore they do not affect niche and fitness differences in two-species communities (red dashed line). However, they will affect niche and fitness differences in communities with more species, albeit in a potentially complex way. While each higher order interaction affects niche and fitness differences on its own, their effects cancel out (blue line). Similarly, the effects of $\beta_{iii}, \beta_{ijj}, \beta_{jii}$ and β_{jjj} on fitness differences can be explained by their effect on the first-order interactions (Fig. 7.4).

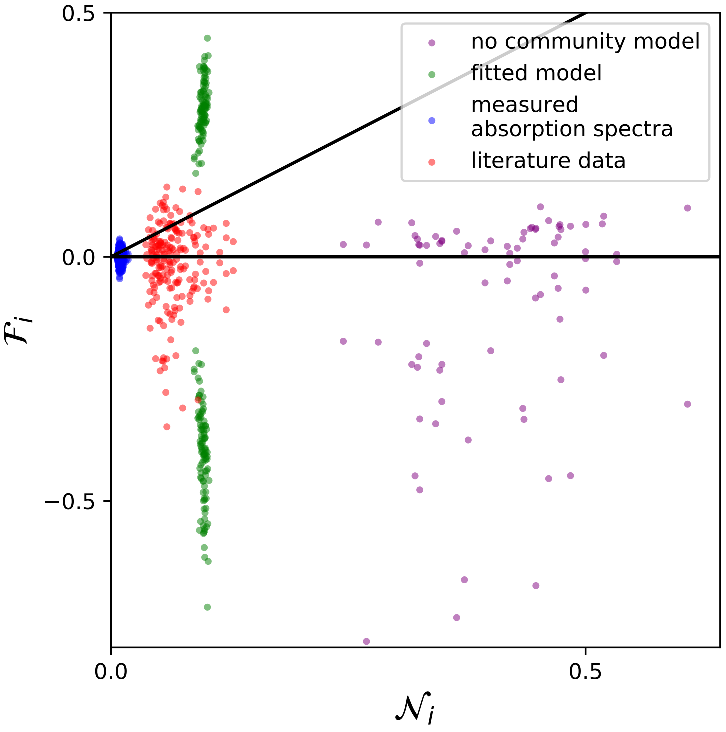

Figure 7.3: Niche differences measured without fitting the Stomp model (purple dots) were much higher than any simulation of the Stomp model. The green dots represent the Stomp model fitted to the experimental data. Blue dots represent the Stomp model with measured absorption spectra but photosynthetic efficiencies as in chapter 5. Red dots represent the Stomp model with all community parameters as in chapter 5. Species above the black line have negative invasion growth rates and will not persist.

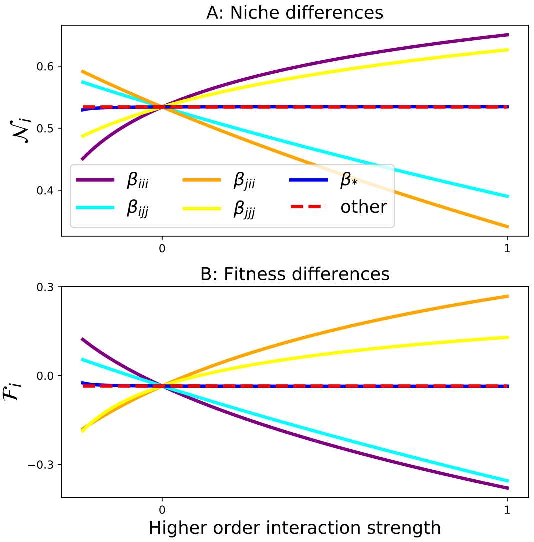

Figure 7.4: Higher order interactions do affect niche (A) and fitness differences (B). Their effect can be understood by their effect on the first-order interactions. A: Higher order interactions that affect intraspecific interactions (β_{iii} and β_{jjj}) increase niche differences similar to α_{ii} and α_{jj}. Higher order interactions that affect interspecific interactions (β_{ijj} and β_{jii}) decrease niche differences. If all higher order interactions have similar strength their effects cancel out (blue line, β_*). The other higher order interactions do not affect niche or fitness differences in two-species communities, as they are only relevant when both species are present. Niche and fitness differences, however, are computed based on monoculture growth rates and invasion growth rates, where only one species is present. B: Higher order interactions that increase species i's sensitivity to competition (β_{iii} and β_{ijj}) decrease the $\mathcal{F}_i$, similar to α_{ii} and α_{ij}. Higher order interactions that increase species j's sensitivity to competition (β_{jjj} and β_{jii}) increase $\mathcal{F}_i$. Again, other higher order interactions do not affect $\mathcal{F}_i$ (red dashed line) and the effects of the various higher order interactions can cancel (blue line).

Computing niche and fitness differences with different community models

Chapter 3 showed that approximations of a community model can affect niche and fitness differences. Implicitly, any fitted community model to empirical data can be seen as an approximation of the real underlying community model. I fitted various community models to the empirical data from chapter 2 to investigate how the model choice can affect our understanding of the community.

To compute niche and fitness differences, I fit two LV models (once including all empirical data red dots, fig. 7.5) and once excluding the densities from experiments with high starting densities, as these are usually not performed (blue dots)), a LV model with higher order interactions (orange dots), the Stomp model (green dots) and computed them without fitting a community model to the densities of the species (purple dots). To incorporate measurement uncertainty, I computed niche and fitness differences by each method 100 times. As expected, the different community models lead to quantitatively different values for niche and fitness differences. However, not only were the differences significant, but the regions were almost completely distinct with no overlap.

In addition to the quantitative differences the different models lead to different qualitative predictions. Both species have positive invasion growth rates, which strongly suggests that they can coexist (Barabás *et al.*, 2018; Turelli, 1978). Niche and fitness differences based on the species densities correctly predict this, as both species are below the persistence line (purple dots). Additionally, it predicts that the two species do not differ significantly in their competitive strength. Conversely, all of the other community models predict that BS5 is the clear competitive dominant species, and one fitted LV model and the Stomp models predict competitive exclusion. Similarly, Godwin *et al.* (2020) found that fitted LV models do not always correctly predict coexistence in both empirical and simulated data. The other LV models as well as the model with higher order interactions show no clear outcome of competition. The LV model based on all empirical data does predict positive frequency dependence in about 30% of the cases. Finally, we see a clear difference between the two fitted LV models, which indicates that not only increasing species to equilibrium but also decreasing species to equilibrium can contain important information about the community processes.

Niche and fitness differences critically depend on the intrinsic and the invasion growth rates. To get precise estimates of niche and fitness differences we need precise estimates of these two growth rates. Fitting a community model to densities, however, implies that growth rates when the species is not rare can affect these two growth rates. The current example shows that this can lead to qualitatively different predictions of coexistence.

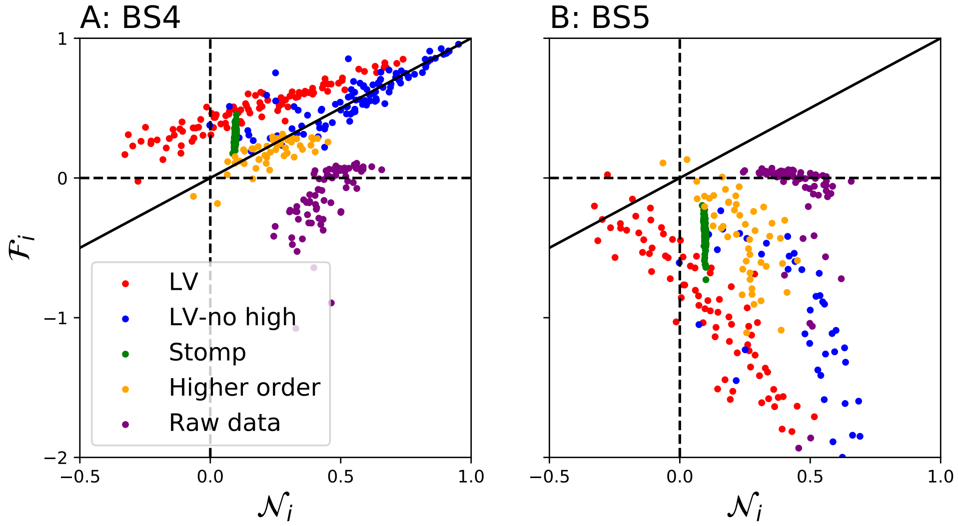

Figure 7.5: Fitting different community models to the same underlying experimental data from chapter 2 yields vast differences in their niche and fitness differences. Niche and fitness differences based on the raw data (purple dots) predicts coexistence and does not show any clear difference in their competitive strength. In contrast, all fitted community models clearly identify the red species as the competitive dominant. Additionally, the fitted LV models and the Stomp model predicts competitive exclusion.

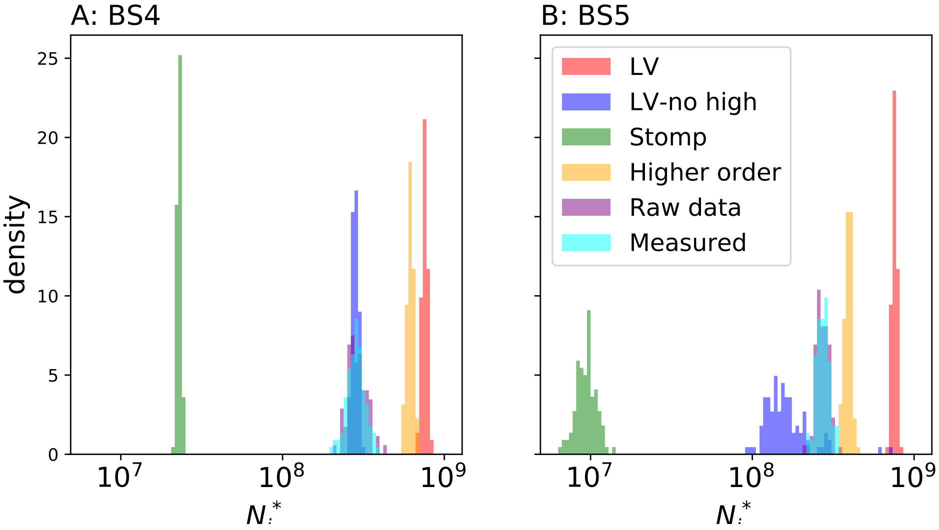

Figure 7.6: The different methods lead to different estimations of the monoculture equilibrium densities. The empirical equilibrium densities are best approximated by the method that does not fit a community model through the empirical data (data only partially visible due to overlap).

Different niche and fitness values show that differences exist, but it is not clear which method best captures the actual niche and fitness differences. It may very well be, that we get a more precise measure of the intrinsic growth rates by including growth rates at higher densities for its computation. Similarly, we get a better estimate of the intercept of a linear regression by increasing the sample size, even if these samples are taken away from the intercept. So far we do not have any golden standard of niche and fitness differences that would allow us to pick the best candidate in this case, we just know that different models can have a huge effect on niche and fitness differences, despite all of them fitting the experimental data very well ($R^2 > 0.9$ for all model fits except the Stomp model).

However, we can test their predictions on other parameters for which we do know how to assess quality. The method based on the raw data best fits the monoculture equilibrium densities of both species (Fig 7.6). The Stomp model underestimates the equilibrium density vastly, and the higher order model as well as the LV model with all data overestimate the equilibrium densities. In conclusion, not fitting a community model to the species densities lead to niche and fitness differences that best meet the coexistence conditions and other parameters.

Obtaining LV models with different methods affects niche and fitness differences

Chapter 4 and 6 both show distributions of niche and fitness differences from different communities. While facilitation is relatively common in the data from chapter 4, facilitation is almost absent in the data from chapter 6. Both chapters use LV models that are fitted to terrestrial plant communities. Therefore, their differences do not arise from points already discussed above. They differ, however, in how the LV models were fitted.

The community models from chapter 6 were fitted exclusively with a regression of species densities over time in two-species sub communities (Hart *et al.*, 2018). That is, in order to obtain μ_i and α_{ii}, the species are all grown in monoculture and the densities are measured over time. A LV model is fit to the densities over time using least squares regressions. To obtain α_{ij} two species are grown together and then the previously obtained community parameters are used to fit α_{ij}. I will refer to this as the regression method from now on.

The community models from chapter 4 were predominantly fit using the relative yield of species in two-species communities. First, all species are grown in monoculture to obtain the monoculture equilibrium density N_i^*, and α_{ii} is set to $1/N_i^*$. The species are then grown in two-species communities to obtain α_{ij} and α_{ji} from the relative yield of each species. Importantly, this method does not include transient dynamics, therefore densities are only measured at the end of the experiment, and μ_i is set to 1.

To obtain the community matrix of a n-species community by any method, one needs to perform on the order of n^2 experiments. The relative yield method has the advantage that densities need not be measured over time. The regression method, on the other hand, allows simulating community densities over time. Additionally, the regression model would allow one to detect that the LV model is not a good approximation of the species interactions. Maynard *et al.* (2019) proposed an integration of these two approaches by first obtaining an estimate of $\mathbf{A}$, potentially by the regression model. This initial approximate of $\mathbf{A}$ is then adjusted such that $\mathbf{A}$ correctly predicts the equilibrium density of the species.

LV models fit by either method lead to approximately the same median for $\mathcal{N}_i$ in two-species communities (regression: 0.84, relative yield: 0.85, Fig 7.7). However, the interquartile range of $\mathcal{N}_i$ is significantly smaller for the regression model (regression: 0.41, relative yield: 0.83, $p \approx 10^{-12}$). As a consequence, facilitation is more probable in community models that were obtained by the relative yield model (regression: 17%, relative yield: 35%).

The differences in $\mathcal{N}_i$ likely stem from differences in the interactions coefficients. Again, the median interspecific interactions strength is comparable

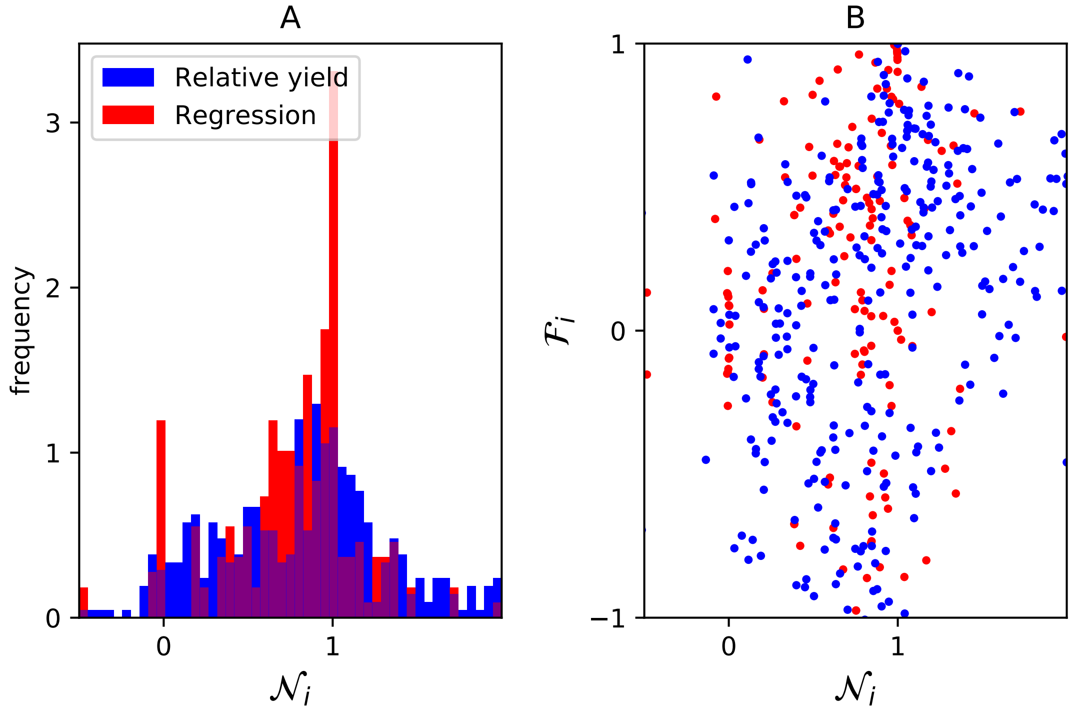

Figure 7.7: A: LV models fitted to relative yield (red) lead to larger spread of $\mathcal{N}_i$ than LV models fitted with regression (blue). The two methods lead, however, to very similar median of $\mathcal{N}_i$. B: As a consequence, the relative yield method leads to higher probability of both mutualism and positive frequency dependence.

between the two methods, but interquartile range is larger for the interaction strengths measured with the relative yield method. This could be interpreted as a larger measurement uncertainty. To obtain the interaction coefficients with the regression model, one fits a community model to the densities over time, i.e. many data-points. Conversely, the interaction coefficients with the relative yield model are based only on the final density, i.e. few data-points, which leads to a higher variance in the estimates.

7.2 Future directions of MCT

7.2.1 Extending our understanding of niche and fitness differences

MCT seeks general patterns that allow species to coexist. Yet most applications of niche and fitness differences focus on linear species interactions, such as LV models or annual plant models with Beverton-Holt competition (Levine & HilleRisLambers, 2009; Adler *et al.*, 2007; Godoy & Levine, 2014; Germain *et al.*, 2016; Saavedra *et al.*, 2017; Godoy *et al.*, 2020; Adler *et al.*, 2018b). This choice a priori rules out the possibility of finding new patterns of coexistence or of finding models in which the current theory fails (Pande *et al.*, 2019). To find new general patterns or confirm the patterns we already know, we must apply modern coexistence theory to a larger set of community models.

Additionally, MCT predominantly focuses on basal species, most notably plants (Godoy *et al.*, 2014; Adler *et al.*, 2018b; Chu & Adler, 2015) or phytoplankton (Narwani *et al.*, 2013; Gallego *et al.*, 2019). We know very little about how guilds from other trophic levels coexist.

Various authors have already called for the inclusion of a broader range of community models into MCT, such as predators (Chesson & Kuang, 2008; Petry *et al.*, 2018), mutualists (Bimler *et al.*, 2018; Johnson & Bronstein, 2019) and multi-trophic networks in general (Godoy *et al.*, 2018). However, all these propose their own framework to understand these new community models. Their frameworks, which are sometimes very specific, lead to an in-detail analysis of the specific community model, however they lack generality. The newly proposed definitions from chapter 2 and 6 provide an alternative solution, in which we exchange detail knowledge of the specific systems for a general understanding that includes many communities.

MCT has primarily focused on basal species and how competition for resources can mediate negative (or positive) frequency dependence (Letten *et al.*, 2017; Chesson, 1990). Chesson & Kuang (2008) demonstrated theoretically that the negative frequency dependence mediated via common predators can be captured into the framework of niche and fitness differences as well. Similarly, Petry *et al.* (2018) investigated empirically the effect of ants on the coexistence of annual plants. However, both assume a priori that the predators persist and do not include them as focal species. Additionally, negative frequency dependence can also be mediated via common mutualists, as shown by Johnson & Bronstein (2019). They model how plant species interact mutualistically with a fungus to exchange resources or how plant species interact with pollinators. However, again, they assume a priori that mutualists persist independently and do not introduce them as focal species.

Both these contributions are essential extensions of MCT, however, comparing them directly is difficult, as they use different frameworks. By using different frameworks and focusing on basal species, they do not extend our understanding of which general patterns allow coexistence in more broad communities.

To compare these two extensions I computed niche and fitness differences (Appendix E.1) and mapped them with one graphical representation for different choices of focal communities (Fig. 7.8). While the new method can in principle analyse all these models, we must first ensure that invasion growth rates correctly predict coexistence. I compute niche and fitness differences for structurally equivalent communities, but once with predator and once with mutualist species (triangles, blue respectively red markers in fig. 7.8). Using three different types of focal community, I investigated 1. how the predators and mutualists coexist, with the basal species seen as resources (Fig. 7.8 A), 2. how the basal species coexist via resource competition and apparent competition (Fig. 7.8 B), and 3. how does the entire community coexist (Fig. 7.8 C). The second focus is the current focus of MCT, albeit MCT usually does not include the predators or mutualists into analysis. I believe that the last focus should be the future direction of MCT. This leads to a total of six different focal communities.

This leads to three insights: First, in all six choices of focal community species coexist because niche differences overcome fitness differences, confirming the main finding of MCT. Second, while structurally very different, predators and mutualists coexist via the same high-level processes. That is, despite them being treated very differently, this short analysis suggests that they could be studied together. Third, when focusing on predators respectively mutualists (cyan ellipse), these compete with each other for the basal species (Fig. 7.8A, $\mathcal{N} < 1$). Yet with slightly different parameter values predators respectively mutualists can facilitate each other ($\mathcal{N} > 1$). This may not be too surprising for mutualists, as they both facilitate the same species. Predators, on the other hand, facilitate each other because the basal species compete with each other for resources. Predator A reduces the density of basal species a, which increases density of basal species b, which facilitates predator B. Note, from the predator's point of view, the apparent competition is just plain resource competition. As a consequence, resource competition can give rise to facilitation.

In this short example, I found that the general conclusions of MCT seem to hold in more general communities. Of course this is only a very limited range of possible community models and structures; further research is needed. But, we also gained new insight into resource competition and how predators and mutualists seem to behave very similarly.

7.2.2 Recent developments of MCT

Recently, three independent advances of MCT have been proposed by Saavedra *et al.* (2017), Ellner *et al.* (2019) and my reinterpretation of niche and fitness differences. These proposed solutions overcome some of these limitations. Here, I want to briefly discuss which limitations they might solve and how they are linked to each other.

As mentioned in the introduction, there are seven main limitations in MCT, all dealing with limiting complexity: (i) MCT depends on analytical mathematics and as a consequence focused on simple community models; (ii) MCT primarily focuses on linear species interactions; (iii) MCT primarily focuses on competitive species interactions; (iv) MCT investigates the coexistence of few species, predominantly two-species communities; (v) There are few collaborations between MCT and related fields; (vi) MCT investigates the coexistence of one trophic level and assumes that species from other trophic levels do not go extinct. As such it does not focus on entire communities, but rather, on sub-communities; (vii) How do we assess coexistence in a community model where invasion growth rates do not correctly predict coexistence? In this section I will focus on how recent advances in MCT solve conceptual problems of MCT, and therefore, I will not comment on challenge (v) further.

The structural approach on coexistence

The structural approach proposed by Saavedra *et al.* (2017) investigates the structural stability of a community model and was originally defined for a LV like community model. Given the interaction matrix $\mathbf{A}$, it defines niche differences as the volume of $D_F(\mathbf{A})$, the set of intrinsic growth rates with a feasible equilibrium point. Fitness differences are defined as the distance of the current intrinsic growth rates to the centre of $D_F(\mathbf{A})$.

The structural approach, as suggested by the name, investigates structural and not dynamical stability. That is, given a species interaction matrix $\mathbf{A}$, it asks how probable it is, that the intrinsic growth rates μ will yield a feasible equilibrium. That is, at it's core, the structural approach focuses on a different question than most of modern coexistence theory. Song *et al.* (2020a) have shown that structural stability and dynamical stability are related, but that increasing one may decrease the other. While originally proposed as an extension of niche and fitness differences, these should therefore not be compared to traditional (dynamical) niche and fitness differences.

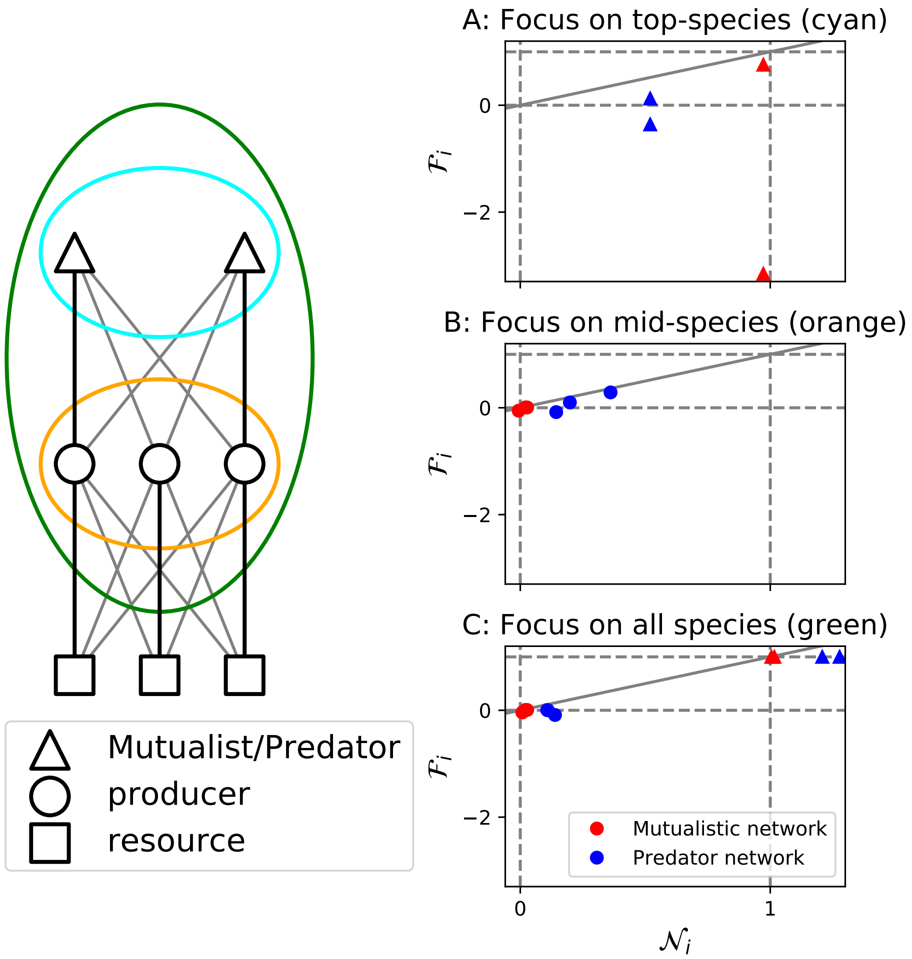

Figure 7.8: In a tri-trophic community MCT typically focuses on the producer level. How can these producers coexist? How is negative frequency dependence governed via resource competition or apparent competition (orange ellipse, left panel). Similarly, we could focus on the top-level only (cyan ellipse), this would advance our understanding of coexistence to some extent yet remain agnostic to the entire picture. Rather, MCT should start to focus on the entire community (green ellipse) and understand how competition but also other trophic interactions shape species coexistence (Godoy *et al.*, 2018). The green ellipse does not include the resources, as these are assumed to be abiotic. A: An alternative focus of MCT, two-species from the top level compete ($\mathcal{N}_i < 1$) and do not depend on other species ($\mathcal{F}_i < 1$). They do not depend on other species, as the underlying species are considered as resources, not species, and thus part of the environment. B: The current focus of MCT , species interact with resource competition. C: The potential future focus of MCT, the investigation of entire communities and how all species can persist. Here the top-level species (red and blue triangles) do depend on other species ($\mathcal{F}_i > 1$) and profit from them ($\mathcal{N}_i > 1$). Comparing C with B or A we see that changing the focus of our study can affect how we interpret the persistence mechanisms for both trophic levels.

The structural approach can efficiently analyse a community containing many interacting species. For any given community, however, the structural approach gives the probability that all species coexist. It does not give any information about which species is most likely to go extinct or whether all species can coexist for the current intrinsic growth rates.

The structural approach has been partially extended to per-capita growth function of the form $\frac{1}{N_i} dN_i dt = f_i(\sum_j \alpha_{ij} N_j)$ where f_i is a monotone function (Cenci & Saavedra, 2018). The structural equivalents of niche and fitness differences are computed by inverting the functions f_i. However, species interactions are still governed by linear interactions ($\sum_j \alpha_{ij} N_j$) and as such, non-linear species interactions can only be integrated to limited amounts. As such, the structural approach offers only a partial solution to challenge (ii).

The structural approach provides a solution to the challenges (iii), (iv) and (vi), as the interaction matrix can contain positive and negative entries. Importantly, the structural approach analyses the coexistence region of the entire population at once and can therefore easily be used to include higher trophic levels into the analysis (Song *et al.*, 2018). It can easily analyse communities with many species, albeit the graphical representation of niche and fitness differences is challenging for four species communities and not possible for communities with more species.

The structural approach benefits from the fact that assessing coexistence is both conceptually and computationally easy in a community with linear species interactions. As such it does not solve challenge (vii), but by focusing on communities where we can assess coexistence, it circumvents the problem.

Expansion of MCT with simulations

The expansion of MCT proposed by Ellner *et al.* (2019) is based on a comparison of different scenarios of the community model in which certain mechanisms are turned on or off. Comparing the community model when the environment fluctuates to a community model when the environment is constant gives insight into how much the environmental variation is essential to coexistence of the species. Ellner *et al.* (2019) focuses on temporal environmental variations and, as such, revolutionised how we understand the storage effect or relative non-linearities. However, it is worth noting that this approach can also be used to understand how certain traits affect coexistence.

This expansion of MCT allows the simulation of a community's key properties, rather than analytical mathematics. In fact, this approach has already been used to analyse storage effect and relative non-linearity in yeast species that are governed by non-linear species interactions (Letten *et al.*, 2018). It therefore solves challenge (i).

The expansion can be used to address multispecies and non-competitive communities as well (challenges (iii) and (iv)). For example, Ellner *et al.* (2019) analysed a community matrix including facilitative species interactions and found that, in this specific case, facilitation was not essential for coexistence. Also, Ellner *et al.* (2019) have used their method to analyse non-linear species interactions (challenge (ii)).

Mathematically, the expansion can be used to analyse multi-trophic communities (challenge (vi)) to some extent. It can analyse communities in which all species are governed by identical functional responses, such as in a LV model. It could not, for example, analyse a community with resource explicit dynamics, where not all species consume exactly the same resources or species. Biologically, the expansion is based on giving all species the average trait of the community. To analyse a community with plants and herbivores, the expansion would create plant-herbivore hybrids. That is, it would assign to plants a trait of how fast they can consume other plants and herbivores would be allowed to do photosynthesis.

The expansion is based on invasion analysis and thus does not advance our assessment of coexistence (challenge (vii)). Importantly, it inherits all the limitations of the invasion analysis. Therefore, it may therefore not be applicable to communities with many species or it may lead to wrong predictions.

Intuitive niche and fitness differences

My own definition of niche and fitness differences has been introduced in much detail in chapter 2 as well as its limitations and benefits. Though, I will repeat them briefly for comparison.

The niche and fitness differences were designed not to depend on analytical mathematics (challenge (i)) and to include non-competitive species interactions (challenge (iii)). Chapters 3 through 6 each address one of the challenges (ii) to (vi). It, however, does not advance our assessment of coexistence, but completely depends on invasion analysis (challenge (vii)).

7.2.3 Future perspectives on MCT

Taken together, the three conceptual advancements of MCT can be used to analyse multi-trophic, multi-species communities with non-linear species interactions. Few empirical applications of these new concepts are already available (Letten *et al.*, 2018; Petry *et al.*, 2018), however, they mainly focused on known community structures (few species, one trophic level).

The remaining challenge is how we can assess coexistence in complex communities. Currently, the most used approach currently, invasion analysis, suf-

challenge	Structural approach	expansion of MCT	Intuitive niche and fitness differences
(i) not analytical	✓	✓	✓
(ii) Non-linearities	linear inter-specific interactions	✓	✓
(iii) Non-competitive	✓	✓	✓
(iv) Multi-species	✓	✓	✓
(vi) multi-trophic communities	✓	creates consumer-producer hybrids	✓
(vii) assessing coexistence	focuses on simple communities	invasion analysis	invasion analysis

Table 7.1: Combined, the three new advancements of MCT solve five of the six main challenges of MCT. MCT can now investigate coexistence in multi-species, multitrophic communities with non-linear species interactions. However, assessing coexistence is still an open challenge in complex communities (challenge (vii)).

fers from three problems (see 1.2.3). First, invasion analysis may not be possible. Invasion analysis perturbs the density of the focal species to zero and sets the remaining species to equilibrium density. However, such an equilibrium density may not exist, most notably in food-chains, where species critically depend on lower trophic levels. Yet, these issues can occur in purely competitive communities as well, a well-known counterexample is the rock-paper-scissor community, where all three species combined can coexist, but not each sub-two-species community. The problem increases in species rich communities; in chapter 4 this occurred in about 25% of all six-species communities. Schreiber (2000) proposed methods that allow using invasion analysis, even when one or more species are extinct in the sub-communities. Essentially, it states that at least one species with zero density must have a positive growth rate when one or more species are at zero density. This solves the first problem.

Second, invasion analysis may not correctly predict coexistence. There are communities in which invasion analysis does not correctly predict coexistence. The most prominent communities contain species with Allee effects, in which the growth rates at invasion are governed by different mechanics than the growth near equilibrium density (Barabás *et al.*, 2018). Again, Schreiber (2000) gives necessary and sufficient conditions for when invasion analysis correctly predicts coexistence, which essentially resolves this second problem.

Third, when it is possible and correctly predicts coexistence, it may not be practical. For example, in a community with 20 species, performing and invasion analysis implies finding the stable equilibrium density of 20 different communities, each containing 19 species. Again, the problem worsens with increasing species richness.

Appendix A

Appendix for chapter 2

A.1 Review

As mentioned in the main text the available definitions all suffer from one or several drawbacks which we want to highlight here in the appendix. Table A.1 summarises many features of the different definitions.

The mathematical equations for each definition are given in the column *Definition*. A subscript i indicates that the parameter is species specific. Note that we log-transformed the definition of Adler *et al.* (2007) to be able to compare the different definitions more consistently. Furthermore we only give the definition for two species for Saavedra *et al.* (2017) , for the multispecies case we refer to their original paper.

The *Range* column explains the range of the definitions for the communities without facilitation and with intraspecific competition being stronger than interspecific (solid rectangle in fig. 1 from the main text). In the Lotka-Voltera and annual-plant setting this means $\alpha_{ij}\alpha_{ji} \leq \alpha_{ii}\alpha_{jj}$. As argued in the main text, this range should be [0,1].

The *Pos. Eff.* contains the range of $\mathcal{N}$ when species do exhibit positive interactions. *Undef* indicates that $\mathcal{N}$ and or $\mathcal{F}$ are not defined for this case, e.g. because one would have to take the square root of a negative number. Numbers in red indicate that the range overlaps with the usual range. The definition of Saavedra *et al.* (2017) is defined for small positive interspecific interactions (for which the range is given), not however for large. The *Comp.* contains the range of $\mathcal{N}$ when interspecific interactions are stronger than intraspecific interactions.

Given the $\mathcal{N}$ and $\mathcal{F}$ values the *Coex.* column indicates what relation must be fulfilled in order to have coexistence. For some definitions the knowledge of $\mathcal{N}$ and $\mathcal{F}$ however is not sufficient to infer coexistence.

The column *Add.* indicates some additional information about the defi-

Source	Definition	Range	Pos. Eff.	Comp.	Coex.	Add.
Chesson 2003	$\mathcal{N} = \overline{\left(\frac{\Delta I - \Delta N}{d}\right)}$ $\mathcal{F}_i = \frac{r_i}{d_i} - \mathcal{N}$	$[-\infty, \infty]$ $[-\infty, \infty]$	$[-\infty, \infty]$	$[-\infty, \infty]$	$-\mathcal{F}_i \leq \mathcal{N}$	1 lim. factor
Carroll et al. 2011	$\mathcal{N} =$1-Mean(sens.) $\mathcal{F} =$Std(sens.)	$[-\infty, 1]$ $[1, \infty]$	Undef.	$[-\infty, 1]$	$\mathcal{F} \leq \frac{1}{1-\mathcal{N}}$	Multi-species
Zhao et al. 2016	$\mathcal{N} = 1 + r_i + r_j$ $\mathcal{F}_i = \log_{10}\left(\frac{K_i}{K_j}\right)$	$[-\infty, \infty]$ $[-\infty, \infty]$	$[-\infty, \infty]$	$[-\infty, \infty]$	None	Scaling
Carmel et al. 2017	$\frac{2-\mathcal{N}}{2\sqrt{1-\mathcal{N}}} = \text{Mean}\left(\frac{r_i}{\mu_i} + 1\right)$ $\mathcal{F} = \left(\text{Std}\left(\frac{r_i}{\mu_i} + 1\right)\right)^2$	$[0, 1]$ $[1, \infty]$	$[0, 1]$	Undef.	$\mathcal{F} \leq \left(\frac{2-\mathcal{N}}{2\sqrt{1-\mathcal{N}}}\right)^2$	Multi-species
Saavedra et al. 2017	$\mathcal{N} = \frac{2}{\pi}\arcsin\left(\frac{\alpha_{ii}\alpha_{jj} - \alpha_{ij}\alpha_{ji}}{\sqrt{\alpha_{ii}^2 + \alpha_{ji}^2}\sqrt{\alpha_{jj}^2 + \alpha_{ij}^2}}\right)$ $\mathcal{F} = \frac{180}{\pi}\arccos\left(\frac{r \cdot r_c}{\lVert r \rVert \cdot \lVert r_c \rVert}\right)$	$[0, 1]$ $[0, 90]$	Undef $[0, 1]$	$\mathcal{N} < 0$	$\mathcal{F} \leq 45 \cdot \mathcal{N}$	Scaling Multi-species
Godoy & Levine 2014	$\mathcal{N} = 1 - \sqrt{\frac{a_{ij}a_{ji}}{a_{ii}a_{jj}}}$ $\mathcal{F}_i = \frac{\lambda_i - 1}{\lambda_j - 1}\sqrt{\frac{a_{ji}a_{jj}}{a_{ij}a_{ii}}}$	$[0, 1]$ $[0, \infty]$	Undef.	$\mathcal{N} < 0$	$\mathcal{F}_i \leq \frac{1}{1-\mathcal{N}}$	Model-specific
Adler et al. 2007	$\mathcal{N}_i = \log\left(\frac{\lambda_j}{1 + \frac{a_{ij}}{a_{jj}}(\lambda_j - 1)}\right)$ $\mathcal{F}_i = \log\left(\frac{\lambda_i}{\lambda_j}\right)$	$[0, \infty]$ $[-\infty, \infty]$	$[0, \infty]$	$\mathcal{N} < 0$	$-\mathcal{F}_i \leq \mathcal{N}_i$	Model-specific
Bimler et al. 2018	$\mathcal{N} = 1 - \frac{e^{a_{ij} + a_{ji}}}{e^{a_{ii} + a_{jj}}}$ $\mathcal{F}_i = \frac{e^{a_{ji} + a_{jj}}}{e^{a_{ii} + a_{ij}}}$	$[0, 1]$ $[0, \infty]$	$[0, 1]$	$\mathcal{N} < 0$	None	Model-specific, Scaling
Chesson 1990	$\mathcal{N} = 1 - \sqrt{\frac{a_{ij}a_{ji}}{a_{ii}a_{jj}}}$ $\mathcal{F}_i = \sqrt{\frac{a_{ji}a_{jj}}{a_{ij}a_{ii}}}$	$[0, 1]$ $[0, \infty]$	Undef.	$\mathcal{N} < 0$	$\mathcal{F}_i \leq \frac{1}{1-\mathcal{N}}$	Model-specific
Chesson & Kuang 2008	$\mathcal{N} = 1 - \frac{\sqrt{\alpha_{ij}^R \alpha_{ji}^R} + \sqrt{\alpha_{ij}^P \alpha_{ji}^P}}{s_i s_j}$ $\mathcal{F}_i = \frac{s_j}{s_i}\frac{\mu_i^R - \mu_i^P - m_i}{\mu_j^R - \mu_j^P - m_j}$	$[0, 1]$ $[0, \infty]$	Undef.	$\mathcal{N} < 0$	$\mathcal{F}_i \leq \frac{1}{1-\mathcal{N}}$	Model-specific
Spaak & DeLaender	$\mathcal{N}_i = \frac{f_i(0, N_j^*) - f_i(N_j^*, 0)}{f_i(0, 0) - f_i(c_j N_j^*, 0)}$ $\mathcal{F}_i = \frac{f_i(N_j^*, 0)}{f_i(0, 0)}$	$[0, 1]$ $[-\infty, 1]$	$\mathcal{N} > 1$	$\mathcal{N} < 0$	$\mathcal{F}_i \leq \frac{\mathcal{N}_i}{1-\mathcal{N}_i}$	-

Table A.1: Summary of the different definitions of $\mathcal{F}$ and $\mathcal{N}$ in the literature. Red entries denote undesirable behaviour. For further explanation see text.

nition. Model-specific indicates that this definition is only applicable to one specific model. The definition of Chesson (2003) is only applicable to models with only one limiting factor (Barabás *et al.*, 2018), as for other models $\mathcal{N}$ and $\mathcal{F}$ depend on the chosen limiting factor. Scaling indicates, that this definition depends on the parametrisation of the model. The easiest way to see this is Zhao *et al.* (2016). If the same experiments were performed twice, once measured in mg and once in μl, the $\mathcal{F}$ would differ, as the two bacteria strains will not have the same physical density ($\frac{mg}{\mu l}$). Similarly in Bimler *et al.* (2018) the values of $\mathcal{N}$ and $\mathcal{F}$ change if we re-parametrise the system to have $\alpha_{ii} = 1$. The structural equivalent of fitness differences in Saavedra *et al.* (2017) is also affected if we re-parametrise to have $r_i = 1$. Finally the definitions of Carroll *et al.* (2011); Carmel *et al.* (2017) and Saavedra *et al.* (2017) can be applied to multispecies communities, however in this case the coexistence condition does not suffice to assess coexistence of the species in a community. That is there might be two communities, that have the same $\mathcal{N}$ and $\mathcal{F}$ values, but the species of one community will coexist, while the species in the other will not.

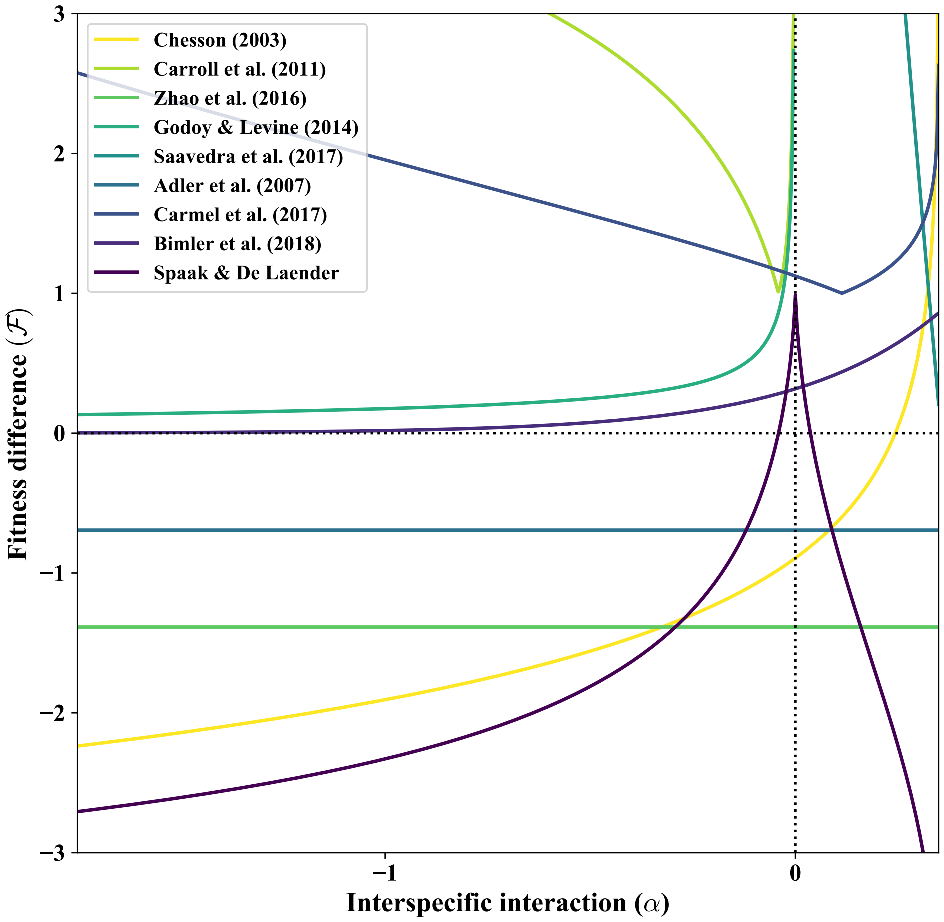

Figure A.1: $\mathcal{F}$ values for the annual plant model according to different definitions for varying interspecific competition $\alpha = -\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}$. Comparing the different definitions of $\mathcal{F}$ is more difficult than comparing the different $\mathcal{N}$, as some definitions interpret $\mathcal{F} = 0$ to be equal fitness while other have $\mathcal{F} = 1$ for equal fitness. For the definition of Chesson (2003) we chose species 1 to be the limiting factor. Parameter values are: $\lambda_1 = 1.5, \lambda_2 = 3, \alpha_{11} = 1, \alpha_{22} = 1, \alpha_{21} = 0.7$ and α_{12} varies in $[-0.5, 2.5]$.

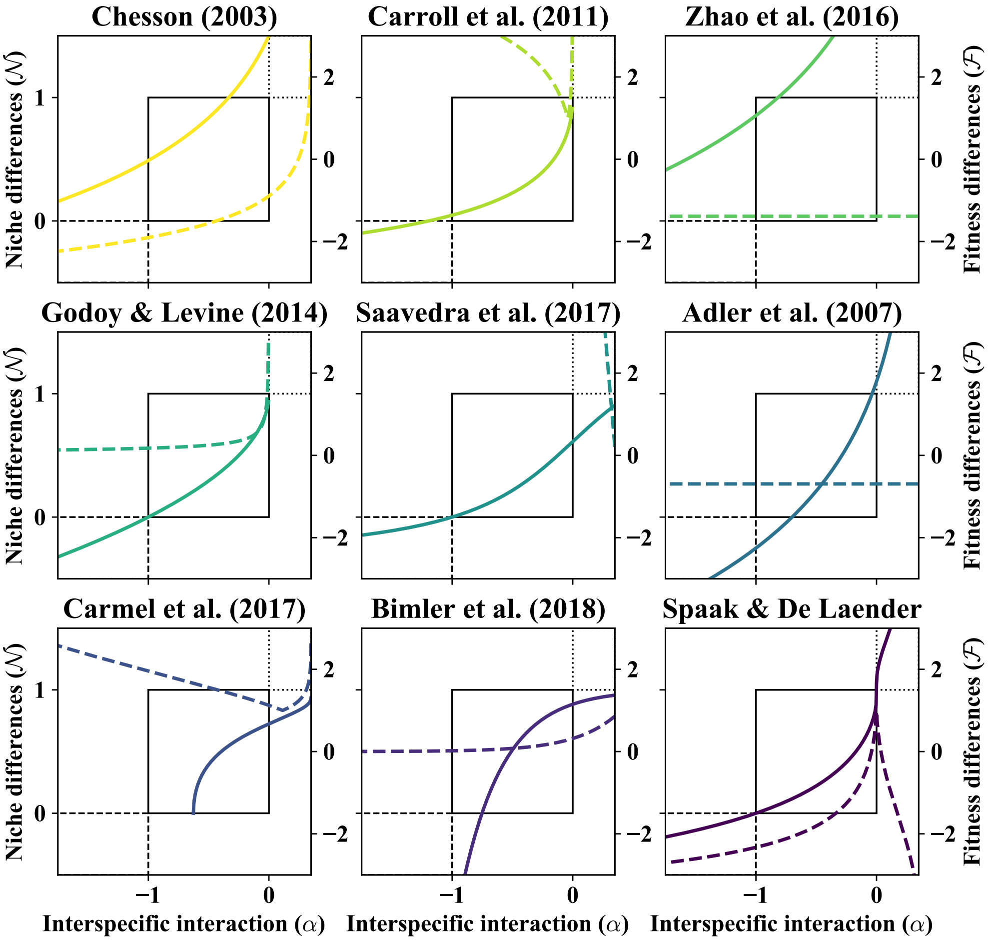

Figure A.2: $\mathcal{N}$ and $\mathcal{F}$ values for the annual plant model according to different definitions for varying interspecific competition $\alpha = -\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}$ per definition. Full lines represent $\mathcal{N}$, dashed lines represent $\mathcal{F}$.

A.2 Mathematical proofs

Before we go into the proofs and special cases we first introduce some appendix specific notation. As in the main text we use the following notation to describe population dynamics:

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, N_j) \tag{A.1}$$

Note that this notation is slightly different from the usual form, which is

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_1, N_2) \tag{A.2}$$

In our notation the density of the focal species is the first argument of the growth function of said species. Opposed to the more conventional natural order of the species, this allows us to more easily write $f_i(0, N_j)$ for the invasion growth rate and similar expressions. The growth rates are assumed to be biological, explicitly we assume

$$1. f_i \text{ are continuous functions in all their arguments} \tag{A.3}$$

$$2. \exists \lim_{N_i \to 0} f_i(N_i, 0) = f_i(0,0) \tag{A.4}$$

$$3. \limsup_{N_i \to \infty} f_i(N_i, N_j) < 0 \tag{A.5}$$

The first assumption is obviously fulfilled for any biological system. The second assumption states that it is reasonable to talk about the monoculture growth rate $f_i(0,0)$. The third assumption ensures that species cannot reach unlimited densities. Those not familiar with the limit supremum can just replace the limit supremum with the normal limit. The limit is taken with fixed but arbitrary N_j. Especially we do not assume that the limit is equal for different N_j or that the limit has to be $-\infty$, nor is anything said about the uniformity of the convergence.

We add the following assumption

$$4. f_i(0,0) > f_i(N_i, 0) \tag{A.6}$$

That is the per capita growth rate in monoculture is maximal at minimal density. While most biological systems fulfill this assumption it is not a biological necessity. It is solely included for mathematical purposes.

Finally we introduce the following notation

$$\mathcal{N}_1(c) = \frac{f_1(0,N_2^*) - f_1(cN_2^*,0)}{f_1(0,0) - f_1(cN_2^*,0)} \tag{A.7}$$

$$\mathcal{N}_2(c) = \frac{f_2(0,N_1^*) - f_2(\frac{1}{c}N_1^*,0)}{f_2(0,0) - f_2(\frac{1}{c}N_1^*,0)} \tag{A.8}$$

Where the niche difference depends on the conversion factor $c = c_2$. We omitted the dependence of c on the species, as we have seen that $c_i = \frac{1}{c_j}$. This definition is asymmetric in the species, however the arbitrary choice that species 1 depends linearly on c only affects c itself, not the $\mathcal{N}$.

A.2.1 Existence of $\mathcal{N}$ and c

We want to solve $|1 - \mathcal{N}_i(c)| = |1 - \mathcal{N}_j(c)|$ for c, we therefore have to prove that such a solution always exists. The solution will be denoted c'. In this part we only prove the existence of c', the uniqueness of such a c' will be discussed below. We first present a "proof" based on biological meaning and logic, that requires a minimum of mathematical knowledge. In this "proof" we omit the absolute values. This biological reasoning is then turned into a rigorous mathematical proof.

The definition of $\mathcal{N}$ compares the interspecific competition ($f_1(0,N_2^*)$) with intraspecific competition ($f_1(cN_2^*,0)$). The intraspecific competition however depends on the conversion factor c, which can take any positive value. The larger this c is, the larger the intraspecific competition will be. By choosing the c being 0 (respectively ∞) intraspecific competition will be very small (large) compared to interspecific competition and hence $\mathcal{N}$ will be $-\infty$ (> 0). The species however react differently to this value c, such that we have a value c'' where $\mathcal{N}_1 < \mathcal{N}_2$ and a value c''' with $\mathcal{N}_2 < \mathcal{N}_1$, therefore there must also be a value, where they are equal.

Theorem 1. $f_i(0,0) \neq f_i(0,N_j^*) \Rightarrow \exists c' : |1 - \mathcal{N}_1(c')| = |1 - \mathcal{N}_2(c')|$

Proof. We define $A_i = \lim_{N\to\infty} f_i(N,0)$. For simplicity we assume the existence of the limit, if this is not given a similar proof can be done with $\limsup$. With this definition we can compute:

$$\lim_{x\to\infty} |1-\mathcal{N}_1(x)| = \left| \lim_{x\to\infty} \frac{f_1(0,0)-f_1(0,N_2^*)}{f_1(0,0)-f_1(xN_2^*,0)} \right| \tag{A.9}$$

$$= \left| \frac{f_1(0,0)-f_1(0,N_2^*)}{f_1(0,0)-\lim_{x\to\infty} f_1(xN_2^*,0)} \right| \tag{A.10}$$

$$= \left| \frac{f_1(0,0)-f_1(0,N_2^*)}{f_1(0,0)-A_1} \right| \tag{A.11}$$

$$< \infty \tag{A.12}$$

$$\lim_{x\to 0} |1-\mathcal{N}_1(x)| = \left| \lim_{x\to 0} \frac{f_1(0,0)-f_1(0,N_2^*)}{f_1(0,0)-f_1(xN_2^*,0)} \right| \tag{A.13}$$

$$= |f_1(0,0)-f_1(0,N_2^*)| \lim_{y\to f_1(0,0)} \frac{1}{|f_1(0,0)-y|} \tag{A.14}$$

$$= \infty \tag{A.15}$$

With similar arguments we get $\lim_{c\to 0} 1-\mathcal{N}_2(c) < \infty, \lim_{c\to\infty} \mathcal{N}_2(c) = \infty$. By the intermediate value theorem we therefore have the existence of a c' with equality. □

Now to the special case $f_i(0,0) = f_i(0,N_j^*)$. This implies $\mathcal{N}_i = 1$ independent of our choice of c. If it happens to be that we also have $f_j(0,0) = f_j(0,N_i^*)$ we also have $\mathcal{N}_j = 1$ for all c, which solves the problem. However in this case we can't compute the c and hence not compute the $\mathcal{F}$. We therefore define $\mathcal{F} = 1$ for both species in this case.

In general, however, we will have $f_j(0,0) \neq f_j(0,N_j^*)$. The equation to be solved then becomes $\left|\frac{f_j(0,0)-f_j(0,N_i^*)}{f_j(0,0)-f_j(cN_i^*,0)}\right| = 0$, which has the "solution" $f_j(cN_i^*,0) = -\infty, c = \infty$. All we therefore have to allow is setting $c = \infty$. With this we can compute $\mathcal{F}_i = \frac{f_i(\frac{1}{\infty}N_j^*,0)}{f_i(0,0)} = 1$ and $\mathcal{F}_j = \frac{f_j(\infty,0)}{f_j(0,0)} = -\infty$. We implicitly assume that $\lim_{N\to\infty} f_i(N,0) = -\infty$, which seems to be a biologically reasonable assumption. This is equivalent to previous definitions (Carroll *et al.*, 2011; Chesson, 2000; Godoy & Levine, 2014). Note that the coexistence condition $-\mathcal{F}_j \leq \frac{\mathcal{N}_j}{1-\mathcal{N}_j}$ becomes useless, as both sides are ∞.

A.2.2 Uniqueness of $\mathcal{N}$ and c

In general the equation $|1-\mathcal{N}_i(c)| = |1-\mathcal{N}_j(c)|$ might not have a unique solution c' but rather multiple solutions c'_k. The equation $|1-\mathcal{N}_i(c)| = |1-\mathcal{N}_j(c)|$

can be arbitrarily complicated, such that in general we can't tell in advance whether there is a unique solution. However we can give a sufficient condition under which the solution is unique, this condition also happens to be biologically meaningful: If both species have strictly negative density dependencies in monoculture (a usual assumption in modern coexistence theory), then the c' and also the $\mathcal{N}$ will be unique. Essentially the monotonicity of the monoculture per capita growth rates $\frac{\partial f_i(N_i,0)}{\partial N_i} < 0$ translates into a monotonicity of $1 - \mathcal{N}_i$, by this monotonicity there can be only one c' with equality.

Theorem 2. *If we assume that* $\frac{\partial f_i(N_i,0)}{\partial N_i} < 0$ *and* $\frac{\partial f_j(N_j,0)}{\partial N_j} < 0$ *then the definition of* $\mathcal{N}_i$ *and of* c' *is unique.*

Proof. We simply have to compute the derivative:

$$\frac{d|1-\mathcal{N}_1(x)|}{dx} = \frac{d}{dx}\left(\frac{|f_1(0,0) - f_1(0,N_2^*)|}{|f_1(0,0) - f_1(xN_2^*,0)|}\right) \tag{A.16}$$

$$= |f_1(0,0) - f_1(0,N_2^*)| \cdot (-1) \tag{A.17}$$

$$\cdot \left(f_1(0,0) - f_1(xN_2^*,0)\right)^{-2} \cdot (-1)\frac{\partial f_1}{\partial N_1} \cdot N_2^* \tag{A.18}$$

$$= N_2^* \frac{|f_1(0,0) - f_1(0,N_2^*)|}{(f_1(0,0) - f_1(xN_2^*,0))^2}\frac{\partial f_1}{\partial N_1} < 0 \tag{A.19}$$

We removed the absolute values from $f_i(0,0) - f_i(xN_2,0)$, as this is always positive according to assumption 4. With similar computation we see that $\frac{d|1-\mathcal{N}_2(x)|}{dx} > 0$ and therefore there exists only one c' □

A.2.3 Multispecies case

The ideas used in the multispecies case are essentially equivalent to the two species case. The growth model is now assumed to have the following shape:

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, \mathbf{N^{-i}}) \tag{A.20}$$

Where $\mathbf{N^{-i}}$ is the vector of all species densities with the density of species i removed. The second argument of f_i will in this part be a vector of dimension $n-1$ and be **bold**. We then define

$$\mathcal{N}_i = \frac{f_i(0,\mathbf{N^{-i,*}}) - f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0})}{f_i(0,\mathbf{0}) - f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0})} \tag{A.21}$$

$$\mathcal{F}_i = \frac{f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0})}{f_i(0,\mathbf{0})} \tag{A.22}$$

with $\mathbf{0}$ is the $n-1$ dimensional 0 vector and $N_j^{-i,*}$ is the equilibrium density of species j (in the presences of the $n-1$ resident species) and c_{ij} is the conversion factor from species j to species i.

The c_{ij} can be found by focusing on the two species sub-communities. That is, for each pair of species we compute the $\mathcal{N}$ of those two species in the presence of all the other species denoted $\mathcal{N}_{ij}$. The presence of the other species is important to include the indirect and higher order effects. However, the densities of the other species are fixed, we only vary the densities of species i and j (essentially the other species are seen as part of the environment). We introduce $\mathbf{N}_{k\neq j}^{-i,*}$, the equilibrium density of the species $k \neq i,j$, in the absence of species i. That is $\mathbf{N}_{k\neq j}^{-i,*}$ is a $n-2$ dimensional vector, that contains the densities of all the species k other than i and j, at the same densities as $\mathbf{N}^{-i,*}$. Note that $\mathbf{N}_{k\neq j}^{-i,*} \neq \mathbf{N}_{k\neq i}^{-j,*}$ in general. With this notation we introduce $f_i'(N_i,N_j) = f_i(N_i,N_j,\mathbf{N}_{k\neq j}^{-i,*})$, i.e. the growth rate of species i, as a function of the densities of species i and j, in the presence of the species $k \neq i,j$. Similarly we define f_j'. The system $f' = (f_i', f_j')$ is a two species community, describing the growth rates of species i and j in the presence of the other species $k \neq i,j$. The densities of the species $k \neq i,j$ remain fixed, for any values of N_i and N_j, however, they are not the same for f_i' and f_j'. By definition we have $f_i'(0,N_j^{-i,*}) = f_i(0,\mathbf{N}^{-\mathbf{i},*})$. Given that f' is a two species community system we can apply the standard definitions to the system, i.e.

$$\mathcal{N}_{ij} = \frac{f_i'(0,N_j^{-i,*}) - f_i(c_{ij}N_j^{-i,*},0)}{f_i(0,0) - f_i(c_{ij}N_j^{-i,*},0)} \tag{A.23}$$

Then we solve the equation $|1-\mathcal{N}_{ij}| = |1-\mathcal{N}_{ji}|$ to obtain c_{ij}. The same proofs for existence and uniqueness apply for the multispecies case.

Given c_{ij} we can compute $\mathcal{N}$ and $\mathcal{F}$ with the equations A.21 and A.22. $\mathcal{N}$ and $\mathcal{F}$ still correctly predict coexistence (see below) and the key intuitions mentioned in the main article still hold. Clearly $\mathcal{N}_i$ is an increasing function in $f_i(0,\mathbf{N}^{-\mathbf{i},*})$, it therefore remains to show, that $\mathcal{N}_i$ correctly interprets the special cases. $\mathcal{N}_i = 1 \Leftrightarrow f_i(0,\mathbf{0}) = f_i(0,\mathbf{N}^{-\mathbf{i},*})$, that is a species has complete niche differentiation, only if the *combined* interspecific interactions are absent. Note however, that this does not imply, that each interspecific interaction is absent. This is only the case if $\mathcal{N}_{ij} = 1$ for all j. $\mathcal{N}_i = 0 \Leftrightarrow f_i(0,\mathbf{N}^{-\mathbf{i},*}) = f_i(\sum_{j\neq i} c_{ij}N_j^{-i,*},\mathbf{0})$, that is a species has complete niche overlap, if individuals of the focal species can be exchanged with species from the non-focal species. Again, this does not mean, that the focal species is interchangable with each other species individually, but rather that as a hole, the community $\mathbf{N^{-i,*}}$ has the same effect as the focal species at density $\sum_{j\neq i} c_{ij} N_j^{-i,*}$.

A.2.4 Decomposition of invasion growthrate

$$\mathcal{N}_i + \mathcal{F}_i - \mathcal{N}_i \cdot \mathcal{F}_i = \frac{f_i(0,N_j^*) - f_i(c_j N_j^*,0)}{f_i(0,0) - f_i(c_j N_j^*,0)} + \frac{f_i(c_j N_j^*,0)}{f_i(0,0)} \tag{A.24}$$

$$- \frac{f_i(0,N_j^*) - f_i(c_j N_j^*,0)}{f_i(0,0) - f_i(c_j N_j^*,0)} \cdot \frac{f_i(c_j N_j^*,0)}{f_i(0,0)} \tag{A.25}$$

$$= \frac{f_i(0,N_j^*) f_i(0,0) - f_i(c_j N_j^*,0) f_i(0,0)}{(f_i(0,0) - f_i(c_j N_j^*,0)) f_i(0,0)} \tag{A.26}$$

$$+ \frac{f_i(c_j N_j^*,0) f_i(0,0) - f_i(c_j N_j^*,0)^2}{(f_i(0,0) - f_i(c_j N_j^*,0)) f_i(0,0)} \tag{A.27}$$

$$- \frac{f_i(0,N_j^*) f_i(c_j N_j^*,0) - f_i(c_j N_j^*,0)^2}{(f_i(0,0) - f_i(c_j N_j^*,0)) f_i(0,0)} \tag{A.28}$$

$$= \frac{f_i(0,N_j^*) f_i(0,0) - f_i(0,N_j^*) f_i(c_j N_j^*,0)}{(f_i(0,0) - f_i(c_j N_j^*,0)) f_i(0,0)} \tag{A.29}$$

$$= \frac{f_i(0,N_j^*)}{f_i(0,0)} \tag{A.30}$$

This derivation also holds for the multispecies case via $f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \mathbf{0}) \mapsto f_i(c_j N_j^*,0)$, $f_i(0,\mathbf{0}) \mapsto f_i(0,0)$ and $f_i(0,\mathbf{N^{-i,*}}) \mapsto f_i(0,N_j^*)$.

A.3 Conversion factors c_i

The conversion factors c_i presented in this work must not be confused with the scaling factors d_i known from previous work (Chesson, 1994, 2003; Barabás *et al.*, 2018; Ellner *et al.*, 2019). In this comparison we limit ourselves to the work of Barabás *et al.* (2018). c_i and d_i differ quite substantially: *Interpretation*: The conversion factors c_i are linked to the total dependence on limiting factors. They are chosen such that one species j has the same total effect on limiting factors as c_j species i. The scaling factors d_i on the other hand are chosen such that the term $\Delta\rho_i$, i.e. the niche partitioning, disappears from the partitioning of the invasion growth rate. They are not directly linked to any mechanistic understanding of the community dynamics. *Existence and uniqueness*: c_i are always well defined (see Existence of $\mathcal{N}$ and c). They are unique, when species have negative density dependence in monoculture, however, when species exhibit intraspecific facilitation multiple values of c_i may exist. d_i work best, when the community is governed by one limiting factor, in this case the d_i are well defined and unique. In all other cases d_i are not unique, may not exist and may not be chosen such that $\Delta\rho_i = 0$. *Applicability*: Both theories can in principal be applied to any community model in which invasion growth rates correctly predict coexistence. However, c_i are most useful in communities without fluctuations with multiple limiting factors. d_i on the other hand are most useful in communities with only one limiting factor and fluctuating environments. *Structure and symmetry*:c is a $n \times n$ matrix with positive entries (in special cases entries 0 and ∞ are possible too). The diagonal entries of c are all one (i.e. $c_{ii} = 1$). Furthermore, the matrix c has a symmetry of the sort $c_{ij} = c_{ji}^{-1}$. d is a $n \times n$ matrix too, but with any entry (i.e. positive and negative). The diagonal entries must be positive. d has no additional structure.

A.4 Examples

A.4.1 Mac-Arthur resource model

First we deduce the Lotka-Volterra model from the resource model of MacArthur (1970).

As stated in the main text, the growth rates for the consumer species and the resources respectively are:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_{l=1}^{m} u_{il}R_l - m_i \tag{A.31}$$

$$\frac{1}{R_l}\frac{dR_l}{dt} = K_l - R_l - \sum_{i=1}^{n} u_{il}N_i \tag{A.32}$$

Where N_i is the consumer density, u_{il} is the rate at which species i consumes resource l, R_l is the density of resource l, and m_i is the loss rate and K_l is the carrying capacity.

We assume that the dynamics of R_l are much faster than the dynamics of N_i, that is we explicitly assume that R_l is always at equilibrium, i.e. $R_l =$

$K_l - \sum_{j=1}^{n} u_{jl} N_j$. Inserting this into the species growth rates we get:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_{l=1}^{m} u_{il}\left(K_l - \sum_{j=1}^{n} u_{jl} N_j\right) - m_i \tag{A.33}$$

$$= \sum_{l=1}^{m} u_{il} K_l - m_i - \sum_{l=1}^{m}\sum_{j=1}^{n} u_{jl} u_{il} N_j \tag{A.34}$$

$$= \underbrace{\sum_{l=1}^{m} u_{il} K_l - m_i}_{\mu_i} - \sum_{j=1}^{n} N_j \underbrace{\sum_{l=1}^{m} u_{il} u_{jl}}_{\langle u_i, u_j\rangle} \tag{A.35}$$

$$= \mu_i - \sum_{j=1}^{n} \langle u_i, u_j\rangle N_j \tag{A.36}$$

Usually the species specific interaction $\langle u_i, u_j\rangle$ is denoted α_{ij} in the Lotka-Volterra model, however, we choose the scalar product notation because it gives a clear biological interpretation of $\mathcal{N}$, $\mathcal{F}$ and c. We continue to compute the $\mathcal{N}$ and $\mathcal{F}$ for the *two* species case (for multispecies case see Appendix D, Multispecies): The monoculture equilibria are $N_i^* = \frac{\mu_i}{\alpha_{ii}}$ and the $\mathcal{N}(c)$ (using $f_i(N_i, N_j) = \mu_i - \sum_{j=1}^{n} \langle u_i, u_j\rangle N_j$):

$$\mathcal{N}_1(c) = \frac{\left(\mu_1 - \frac{\langle u_1, u_2\rangle}{\langle u_2, u_2\rangle}\mu_2\right) - \left(\mu_1 - c\frac{\langle u_1, u_1\rangle}{\langle u_2, u_2\rangle}\mu_2\right)}{\mu_1 - \left(\mu_1 - c\frac{\langle u_1, u_1\rangle}{\langle u_2, u_2\rangle}\mu_2\right)} \tag{A.37}$$

$$= \frac{-\frac{\langle u_1, u_2\rangle}{\langle u_2, u_2\rangle}\mu_2 + c\frac{\langle u_1, u_1\rangle}{\langle u_2, u_2\rangle}\mu_2}{c\frac{\langle u_1, u_1\rangle}{\langle u_2, u_2\rangle}\mu_2} = 1 - \frac{1}{c}\frac{\langle u_1, u_2\rangle}{\langle u_1, u_1\rangle} \tag{A.38}$$

$$\mathcal{N}_2(c) = 1 - c\frac{\langle u_2, u_1\rangle}{\langle u_2, u_2\rangle} \tag{A.39}$$

Solving for c yields $c = \frac{\|u_2\|}{\|u_1\|}$, remember that $c = c_2$, i.e. we have $c_i = \frac{\|u_i\|}{\|u_j\|}$. Which in turn gives $\mathcal{N}_1 = \mathcal{N}_2 = 1 - \frac{\langle u_1, u_2\rangle}{\|u_1\|\cdot\|u_2\|}$, where $\|u_i\| = \sqrt{\langle u_i, u_i\rangle}$. Note that this definition is equivalent to Chesson (1990) but a completely independent proof with a different interpretation. The fitness differences are $\mathcal{F}_i = 1 - \frac{\mu_j}{\mu_i}\frac{\|u_i\|}{\|u_j\|}$, which is equivalent, but not identical. The fitness differences by Chesson (1990) are $\frac{\mu_j}{\mu_i}\frac{\|u_i\|}{\|u_j\|}$.

A.4.2 General resource uptake model

In the previous section we showed that $c_i = \frac{\|u_i\|}{\|u_j\|}$ scales the total resource consumption of the two species in the MacArthur resource model. In this section we assume a more general version of a resource specific model and show that c_i scales the resource uptake of both species. We assume the following growth rates for the species and the resources:

$$\frac{1}{N_i}\frac{dN_i}{dt} = g_i(u_i(R)) - m_i \tag{A.40}$$

$$\frac{dR_l}{dt} = G_l(R) - \sum_i u_i^l(R)N_i \tag{A.41}$$

Where $u_i^l(R)$ is the per capita consumption of resource l by the species i. $u_i(R) = (u_i^l(R))_l$ is the vector containing the consumption of all resources. g_i is the conversion of resources eaten by the species into biomass, m_i is the mortality rate of the species and G_l is the regeneration function of the resource R_l, which may depend on the densities of the other resources. We assume that the only interaction between species and resources is consumption and species interact only indirectly with each other via depletion of resources. Furthermore we assume that the dynamics of the resources are much faster and the density of the resources are always in equilibrium, denoted $R^*(N)$. Finally we assume that the functions u_i,g_i and R^* are monotone, more specifically, the more resources there are, the more the species consumes, the more it consumes the faster it growth (i.e. $\frac{\partial g_i}{\partial R_l} \geq 0$ and $\frac{\partial u_i^l}{\partial R_{l'}} \geq 0$). On the other hand the higher the species densities the lower the resource levels (i.e. $\frac{\partial R_l^*}{\partial N_{i,j}} \leq 0$).

As we do not take any more specific assumptions on the functions g_i,u_i and G_l we can't compute c_i explicitly to proof that c_i scales the total amount of resources consumed. Instead we ask whether c_i increases when species i consumes more. Implicitly the resource uptake functions u_i depends on traits t_j^i. We focus on one specific trait t_1 and assume that higher values of this trait imply higher consumption (i.e. $\frac{\partial u_i^l}{\partial t_1} > 0$). We show that a species i' which consumes more (i.e. $t_1' > t_1$) will have a lower c_i (i.e. $\frac{\partial c_i}{\partial t_1} < 0$) using the implicit function theorem. The parameter c_i therefore becomes a function of t_1.

c_i^0 and t_1^0, the original values for c_i and the trait t_1, are a solution to the following equation

$$1-\frac{f_i(0,0)-f_i(0,N_j^*)}{f_i(0,0)-f_i\left(\frac{N_j^*}{c_i},0\right)}=1-\frac{f_j(0,0)-f_j(0,N_i^*)}{f_i(0,0)-f_i(c_iN_i^*,0)} \tag{A.42}$$

$$\underbrace{\frac{g_i(u_i(t_1,K))-g_i(u_i(t_1,R^*_{t_1}(0,N_j^*)))}{g_i(u_i(t_1,K))-g_i(u_i(t_1,R^*_{t_1}(c_i^{-1}N_j^*,0)))}}_{h_i(c_i,t_1)}=\underbrace{\frac{g_j(u_j(K))-g_j(u_j(R^*_{t_1}(0,N_i^*(t_1))))}{g_j(u_j(K))-g_j(u_j(R^*_{t_1}(c_iN_i^*(t_1),0)))}}_{h_j(c_i,t_1)} \tag{A.43}$$

Hence we define $h(c_i,t_1)=h_i(c_i,t_1)-h_j(c_i,t_1)$. We know that $h\left(c_i^0,t_1^0\right)=0$ and we can therefore use the implicit function theorem to compute $\frac{\partial c_i}{\partial t_1}=-\left(\frac{\partial h}{\partial c_i}\right)^{-1}\frac{\partial f}{\partial t_1}$.

$$\frac{\partial h_i}{\partial c_i}=-\frac{g_i(u_i(t_1,K))-g_i(u_i(t_1,R^*_{t_1}(0,N_j^*)))}{\Big(g_i(u_i(t_1,K))-g_i(u_i(t_1,R^*_{t_1}(c_i^{-1}N_j^*)))\Big)^2} \tag{A.44}$$

$$\cdot\frac{\partial}{\partial c_i}\Big(g_i(u_i(t_1,R^*_{t_1}(c_i^{-1}N_j^*,0)))\Big) \tag{A.45}$$

The first factor is always positive as $K>R^*_{t_1}(0,N_j^*)$. The second factor is positive, as increasing c_i decreases species abundances $(c_i^{-1}N_j^*)$, which increases resource abundance $(R^*_{t_1})$, which increases resource consumption (u_i), which increases biomass accumulation(g_i), hence $\frac{\partial h_i}{\partial c_i}<0$. Similar arguments show that $\frac{\partial h_j}{\partial c_i}>0$ and hence $\frac{\partial h}{\partial c_i}=\frac{\partial h_i}{\partial c_i}-\frac{\partial h_j}{\partial c_i}<0$.

To compute $\frac{\partial h_i}{\partial t_1}$ we take the following assumption

$$\frac{\partial}{\partial t_1}\Big(g_i(u_i(t_1,R^*_{t_1}(0,N_j^*)))\Big)>\frac{\partial}{\partial t_1}\Big(g_i(u_i(t_1,R^*_{t_1}(c_i^{-1}N_j^*,0)))\Big) \tag{A.46}$$

In the left hand side increasing t_1 will increase the consumption and therefore the conversion to biomass. However on the right hand side increasing t_1 will decrease the resource levels, as species i will consume more. This leads to $\frac{\partial h_i}{\partial t_1}<1$. Similarly we can show that $\frac{\partial h_j}{\partial t_1}>1$ which leads to $\frac{\partial h}{\partial t_1}<0$. As a consequence we have $\frac{\partial c}{\partial t_1}=-\left(\frac{\partial h}{\partial c}\right)^{-1}\cdot\frac{\partial h}{\partial t_1}<0$, i.e. under the assumptions taken, higher consumption of resources leads to lower c_i and therefore c_i can be seen as a scaling factor between the total amount of resources consumed of the two species.

A.4.3 Positive interspecific interactions

Generating a resource implies that a species has a negative utilisation of that resource (similar for limiting predator efficacy), which would correspond to a negative bar in figure 2. If the total effect of species j on species i is positive (facilitation), then species j positively affects the limiting factors. c_j is a measure of how *much* species j affects the environment, independent of whether such an effect is positive or negative. We can therefore obtain c_j by making the absolute values of the effects on the limiting factors equal, i.e. $|1-\mathcal{N}_i| = |1-\mathcal{N}_j|$.

To investigate the case where one species facilitates the other we tweak the resource model slightly by allowing species 1 to generate a resource P that can be used by species 2 for its growth. The differential equations become

$$\frac{1}{N_1}\frac{dN_1}{dt} = \left(\sum_{l=1}^{m} u_{1l}R_l - m_1 - p_1\right) \tag{A.47}$$

$$\frac{1}{N_2}\frac{dN_2}{dt} = \left(\sum_{l=1}^{m} u_{2l}R_l - m_2 + u_{2p}P\right) \tag{A.48}$$

$$\frac{1}{R_l}\frac{dR_l}{dt} = K_l - R_l - \sum_{i=1}^{n} u_{il}N_i \tag{A.49}$$

$$\frac{dP}{dt} = p_1N_1 - u_{2p}N_2P - kP \tag{A.50}$$

The parts in red are different from the usual Mac Arthur model. Species 1 creates resource P with efficiency p_1, we from now on however will assume that p_1 is incorporated into m_1 and omit it. u_{2p} is the utilisation of P by species 2 and k is the decay rate of P. We again assume, that the usual resources and the resource P are at equilibrium, which leads to the following equations (for better readability we set $\alpha_{ij} = \langle u_i, u_j\rangle$):

$$\frac{1}{N_1}\frac{dN_1}{dt} = (\mu_1 - \alpha_{11}N_1 - \alpha_{12}N_2) \tag{A.51}$$

$$\frac{1}{N_2}\frac{dN_2}{dt} = \left(\mu_2 - \alpha_{21}N_1 - \alpha_{22}N_2 + u_{2p}\frac{p_1N_1}{k + u_{2p}N_2}\right) \tag{A.52}$$

Solving $1 - \mathcal{N}_1 = 1 - \mathcal{N}_2$:

$$1 - \frac{\mu_1 - \left(\mu_1 - \alpha_{12}\frac{\mu_2}{\alpha_{22}}\right)}{\mu_1 - \left(\mu_1 - c\alpha_{11}\frac{\mu_2}{\alpha_{22}}\right)} = 1 - \frac{\mu_2 - \left(\mu_2 - (\alpha_{21} - \frac{u_{2p}p_1}{k})\frac{\mu_1}{\alpha_{11}}\right)}{\mu_2 - \left(\mu_2 - \frac{1}{c}\alpha_{22}\frac{\mu_1}{\alpha_{11}}\right)} \tag{A.53}$$

$$\frac{\alpha_{12}\frac{\mu_2}{\alpha_{22}}}{c\alpha_{11}\frac{\mu_2}{\alpha_{22}}} = \frac{\left(\alpha_{21} - \frac{u_{2p}p_1}{k}\right)\frac{\mu_1}{\alpha_{11}}}{\frac{1}{c}\alpha_{22}\frac{\mu_1}{\alpha_{11}}} \tag{A.54}$$

$$\frac{\alpha_{12}}{c\alpha_{11}} = c\frac{\alpha_{21} - \frac{u_{2p}p_1}{k}}{\frac{1}{c}\alpha_{22}} \tag{A.55}$$

$$c = \sqrt{\frac{\alpha_{22}\alpha_{12}}{\alpha_{11}\left(\alpha_{21} - \frac{u_{2p}p_1}{k}\right)}} \tag{A.56}$$

So far this result is only applicable when we assume that $\alpha_{21} - \frac{u_{2p}p_1}{k} \geq 0$, that is we have $f_2(0,0) \geq f_2(0, N_1^*)$ and we are still in the realm of the usual definition. Translating this equation back to the mechanistic model we get $c = \frac{\|u_2\|}{\|u_1\|\sqrt{1-\frac{u_{2p}p_1}{k\langle u_1,u_2\rangle}}}$, i.e. resource P should indeed be seen as a negative resource and the total amount of resources consumed by species 1 is $\|u_1\|^2 \cdot (1-\frac{u_{2p}p_1}{k\langle u_1,u_2\rangle})$.

As we have seen in the previous example, the conversion factor are chosen such that both species consume the same total amount of resources. They can however only scale the amount of resources used by a species and not change the sign of the total resources used. In the case $1 - \frac{u_{2p}p_1}{k\langle u_1,u_2\rangle} < 0$ species 1 consumes a negative amount of resources. The conversion factor c can therefore not equate the total amount of resources used by the two species. We therefore equate the absolute value of the total amount of resources used by the two species and therefore also equate $|1 - \mathcal{N}_1| = |1 - \mathcal{N}_2|$, which leads to $c = \sqrt{\frac{\alpha_{22}\alpha_{12}}{\alpha_{11}\left|\alpha_{21} - \frac{u_{2p}p_1}{k}\right|}}$. Note however that we only take the absolute value of $1 - \mathcal{N}$ to compute the c, we do not change the definition of $\mathcal{N}$ itself. This leads to the fact, that not both species have the same $\mathcal{N}$. Rather we have $\mathcal{N}_1 = 1 - \sqrt{\frac{\alpha_{12}\left|\alpha_{21} - \frac{u_{2p}p_1}{k}\right|}{\alpha_{22}\alpha_{11}}} = 1 - |1 - \mathcal{N}_2|$.

A.4.4 Multispecies

As an example we will solve the multispecies Lotka Voltera model, described by equation A.36.

$$
\begin{aligned}
\mathcal{N}_{ij} &= \frac{\left(\mu_i - \sum_{k\neq i}\alpha_{ik}N_k^{-i,*}\right) - \left(\mu_i - \sum_{k\neq i,j}\alpha_{ik}N_k^{-i,*} - \alpha_{ii}c_{ij}N_j^{-i,*}\right)}{\left(\mu_i - \sum_{k\neq i,j}\alpha_{ik}N_k^{-i,*}\right) - \left(\mu_i - \sum_{k\neq i,j}\alpha_{ik}N_k^{-i,*} - \alpha_{ii}c_{ij}N_j^{-i,*}\right)} && \text{(A.57)}\\
&= \frac{(\alpha_{ii} - \alpha_{ij}N_j^{-i,*}}{c_{ij}\alpha_{ii}N_j^{-i,*}} && \text{(A.58)}\\
&= 1 - \frac{\alpha_{ij}}{c^i_j\alpha_{ii}} && \text{(A.59)}
\end{aligned}
$$

Setting the density of species j to zero was done by summing only over the indexes $k \neq i, j$ in the respective function evaluations. Similar to the two species case we have $c^i_k = \frac{1}{c^k_i}$ and hence $c^i_k = \sqrt{\left|\frac{\alpha_{kk}\alpha_{ik}}{\alpha_{ii}\alpha_{ki}}\right|}$, $\mathcal{N}_{ik} = 1 - \text{sign}(a_{ik})\sqrt{\left|\frac{\alpha_{ik}\alpha_{ki}}{\alpha_{ii}\alpha_{kk}}\right|}$.

$$
\begin{aligned}
\mathcal{N}_i &= 1 - \frac{\mu_i - \left(\mu_i - \sum_{k\neq i}\alpha_{ik}N_k^{-i,*}\right)}{\mu_i - \left(\mu_i - \sum_{k\neq i}c^i_k\alpha_{ii}N_k^{-i,*}\right)} && \text{(A.60)}\\
&= 1 - \frac{\sum_{k\neq i}\frac{\alpha_{ik}}{a_{ii}}N_k^{-i,*}}{\sum_{k\neq i}c^i_kN_k^{-i,*}} && \text{(A.61)}\\
&= 1 - \frac{\sum_{k\neq i}(1-\mathcal{N}_{ik})c^i_kN_k^{-i,*}}{\sum_{k\neq i}c^i_kN_k^{-i,*}} && \text{(A.62)}
\end{aligned}
$$

That is the $1 - \mathcal{N}_i$ in multispecies community is a weighted sum of the $1 - \mathcal{N}_{ik}$ in two species case.

$$\mathcal{F}_i = \frac{\mu_i - \sum_{k\neq i} c_k^i \alpha_{ii} N_k^{-i^*}}{\mu_i} \tag{A.63}$$

$$= 1 - \frac{1}{\mu_i}\sum_{k\neq i}\sqrt{\left|\frac{\alpha_{ik}}{\alpha_{ki}}\right|}\sqrt{\alpha_{ii}\alpha_{kk}}N_k^{-i,*} \tag{A.64}$$

$$= 1 - \sum_{k\neq i}\frac{\mu_k}{\mu_i}\sqrt{\left|\frac{\alpha_{ik}\alpha_{ii}}{\alpha_{ki}\alpha_{kk}}\right|}\frac{\alpha_{kk}}{\mu_k}N_k^{-i,*} \tag{A.65}$$

$$= 1 - \sum_{k\neq i}(1 - \mathcal{F}_i^k)\frac{N_k^{-i,*}}{N_k^*} \tag{A.66}$$

The two species case can be recovered from the multispeices case by noticing that $N_k^{-i,*} = \frac{\mu_k}{\alpha_{kk}}$.

After this simple example we want to mention some possible pitfalls. We saw that $\mathcal{N}_{ik}$ of two species is unaffected of the presence of other species in the Lotka-Volterra model. This is because the species do not change their foraging strategies because of the presence of the other species, i.e. there are no higher order effects (Grilli *et al.*, 2017). This will however in general not be the case. Same holds true for the conversion factors c_k^i.

A.5 Material and Methods

Experiments were performed in semi-continuous flow through systems in 6-well plates. Light intensity was set at 1500 lux at the top of the 6 well plates and the walls of the wells were painted black to have a unidirectional light gradient (Huisman & Weissing, 1994). The 6 well plates were mounted on a shaker shaking with 150 rpm to have homogenous culture. The experiment was performed at 20°C. Each well was filled with 5ml brackish mineral medium: $NaCl(8.25gl^{-1})$, $MgCl_2 \cdot 6H_2O(0.66gl^{-1})$, $KCl(0.17gl^{-}1)$, $MgSO_4 \cdot 7H_2O$ $(1.16gl^{-1})$, $CaCl_2 \cdot 2H_2O(0.17gl^{-1})$, Na_3-citrate $(4.98mgl^{-1})$, Na_2-EDTA $(0.83mgl^{-1})$, $NaNO_3(1.25gl^{-1})$, Na_2CO_3 $(46.0mgl^{-1})$, trace metal mix $(1.0mgl^{-1})$, $K_2HPO_4 \cdot 3H_2O(33.2mgl^{-1})$, Fe-NH_4-citrate $(4.8mgl^{-1})$ (Stomp *et al.*, 2004). Twice a week (all 84 hours) we added $200\mu l$ distilled water to counteract evaporation and replaced 1ml (20%) of brackish medium. Densities were measured with a flow-cytometer, to distinguish the cells we used an EM-clustering algorithm on the yellow and red fluorescence channels. To inoculate with above equilibrium densities we centrifuged 50ml of culture at 2000g for 20 minutes.

Density measures, code to produce the figure and compute the $\mathcal{N}$ and $\mathcal{F}$ values can be found on https://github.com/juergspaak/NFD_definitions.

Before conducting an experiment, one does not know the equilibrium densities, nor the conversion factors. However, the definitions require measuring the no-niche growth rate, i.e. at $c_jN_j^*f_i(c_jN_j^*,0)$. Now, $c_jN_j^*$ can be greater than or smaller than N_i^*. If $c_jN_j^* < N_i^*$, the high-abundance starting condition is indeed not needed, as species i will cross $c_jN_j^*$ while growing towards its equilibrium during its monoculture growth curve experiment. If $c_jN_j^* > N_i^*$, one needs to grow the species sufficiently well above its equilibrium density to make sure it will at some point have $c_jN_j^*$, at which its growth will then be measured. We repeat that a priori it is not known which one will be largest, $c_jN_j^*$ or N_i^*.

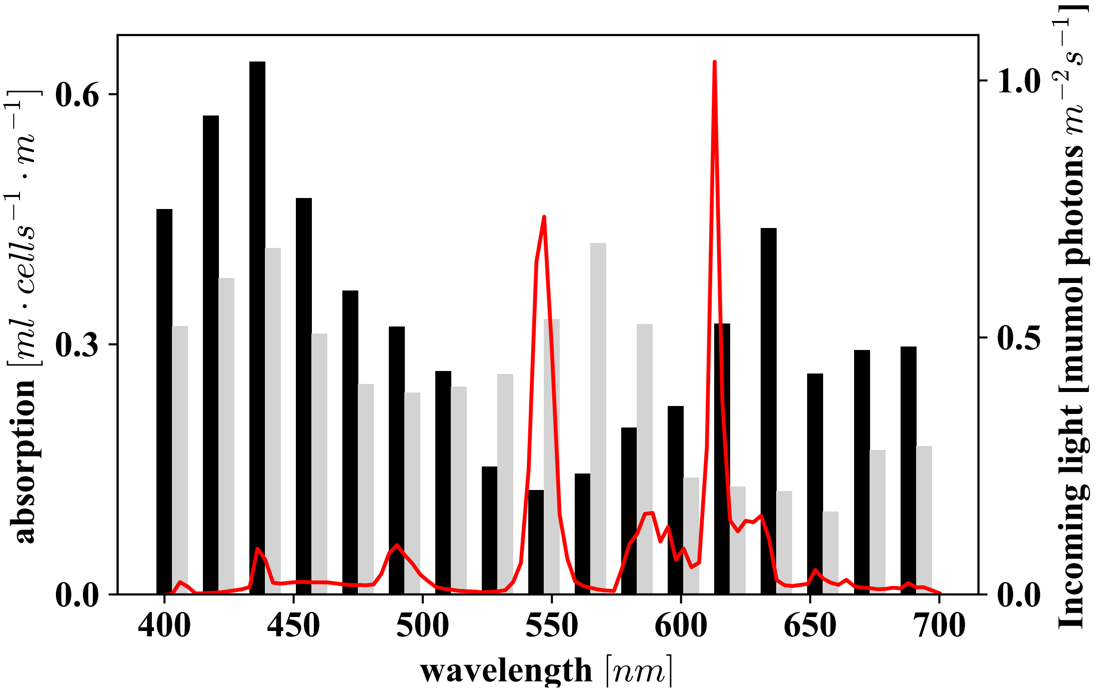

Figure A.3: Absorption spectrum of species 1 (black) and species 2 (grey) and the incoming light intensity used in the experiment. The incoming light comes from a natural-sunlight fluorescent light source.

Appendix B

Appendix for chapter 3

B.1 Resource extinction for substitutional resources

Chesson (1990) and Letten *et al.* (2017) have shown, that the linearisation of the community model and the actual community model have the same conditions for coexistence. However, both proofs implicitly assume, that none of the resources can go extinct. The resources have a logistic growth term in their community dynamics, it is therefore reasonable to assume, that they are biotic and not abiotic resources and may go extinct, which is probable if we assume multiple resource species (Holt, 1977).

We show, that when we relax this assumption, the linearisation potentially does not correctly predict the outcome of coexistence. The core idea is the same for all counter examples, we will explain the idea in more detail for the case where the linear approximation incorrectly predicts priority effects for a community that coexists. We take two sets of resources (a total of four resources, i.e. R_1, R_2, R_3 and R_4), for which the two species compete. If the species would only compete for the first set of resources (R_1 and R_2), they would coexist. Competition only for the second set of resources (R_3 and R_4) leads to priority effects. The supply rates of the resources of the first set are chosen much higher. At equilibrium, the species will therefore only compete for the first set, and coexist. Conversely, the linearisation approach assumes that the species will compete for all resources, independent of species densities and will therefore incorrectly predict priority effects, assuming parameters were chosen correctly. Figure B.1 shows examples where the linear approximation does not correctly predict the outcome of competition.

To see how mortality can affect coexistence, we again take the same set of resources. When mortality is high, then species densities are low and they will not exclude the resources of the second set. As the species compete for all

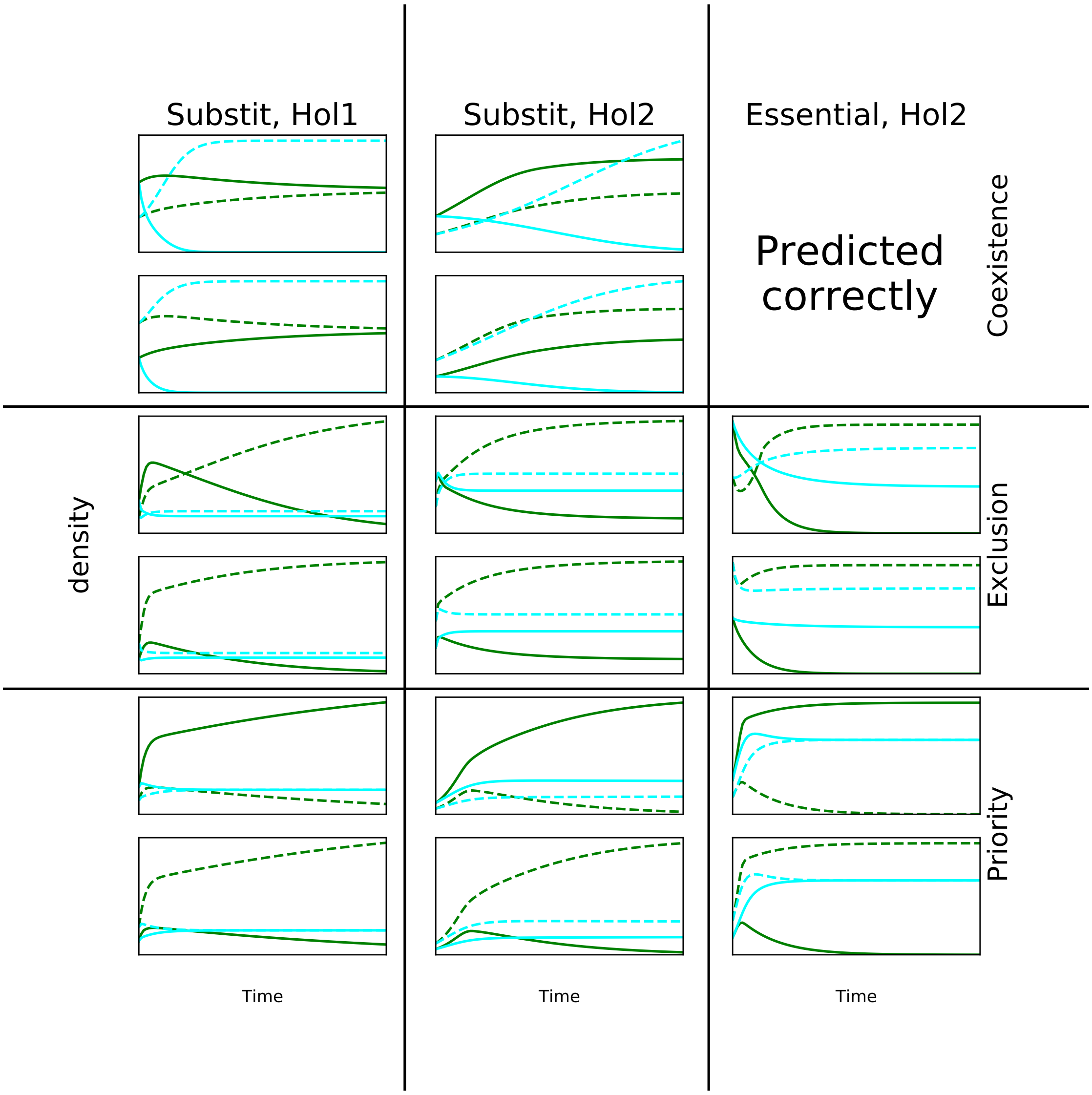

Figure B.1: For each model (colums) and each outcome of competition (rows) we can find parameter settings in which the linear approximation (red) leads to different predictions about coexistence than the full model (blue). The only exception is species competing for essential resources, in which case coexistence is always predicted correctly. However, the linearisation method of this model may predict coexistence for a community with competitive exclusion or priority effects. The linearisation does not correctly predict the outcome of competition, because resources may go extinct. Shown are densities of species one (full line) and species two (dashed) for the full model (green) and the linear approximation (cyan). The two subplots correspond to different starting densities, to distinguish competitive exclusion from priority effects.

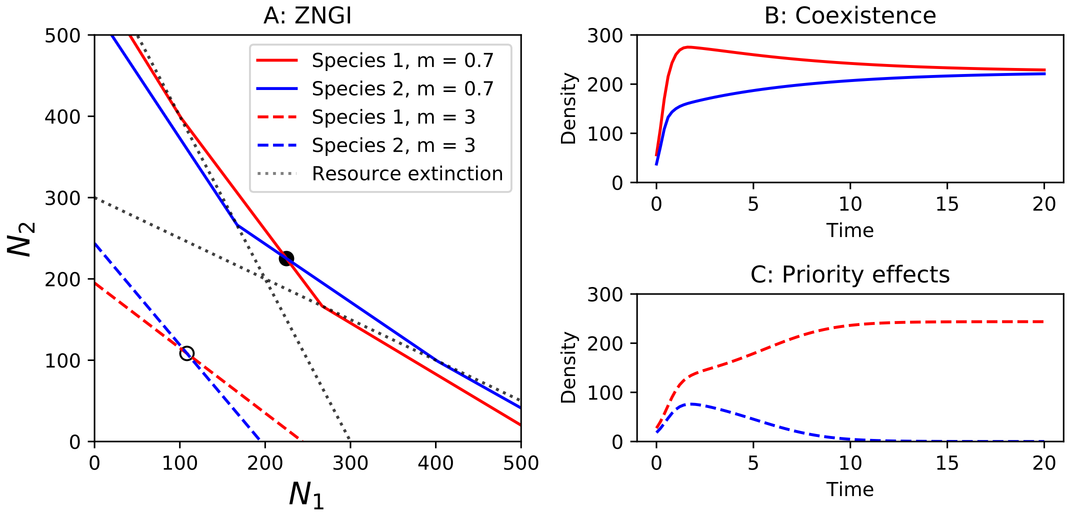

Figure B.2: A: The zero net growth isoclines (ZNGI) for the two species are shown for different mortality rates. Please note, the x and y-axis show densities of the species one and two, not as in the main text the resource densities. The species compete for a total of 4 resources, a visualisation of the ZNGI as a funciton of the resources is therefore not possible (4 dimensional plot). At low mortality (full lines) species reach higher equilibrium densities and two resources go extinct, as the stable equilibrium is above the resource-extinction line. The two species can stably coexist with the remaining two resources. At high mortality (dashed lines) no resources go extinct and the species comete for all resources, leading to priority effects and an unstable equilibrium. B,C: The species densities over time. Species can coexist under low mortality (B), but not under high mortality (C). The two scenarios differ only in their mortality, but as the outcome of coexistence changes from priority effects to coexistence, mortality must affect niche differences.

resources the winner of competition depends on initial densities (priority effects). Priority effects only occur with negative niche differences (Ke & Letten, 2018; Mordecai, 2011). If we reduce mortality, species densities increase and they exclude the resources of the second set and can coexist. Coexistence, however, is only possible with negative niche differences, consequently mortality can affect niche differences.

With a similar idea we create a model with multiple stable equilibria, using six resources, that go extinct under different conditions (Fig. B.3). The species coexist, when they compete for resource 3 and 4. Species one can exclude species two, when they compete for resources 1-4 and species two can exclude species one, when they compete for resources 3-6. Additionally, species one has high consumption rate of the resources 5 and 6, conversely, species two has high consumption rates for resources 1 and 2. When both species are at high density, resources 1,2,5 and 6 are extinct and consequently, the species coexist. When only species one is at high density resources 5 and 6 go extinct and species one excludes species two. When only species two is at high density resources 1 and 2 go extinct and species two excludes species one.

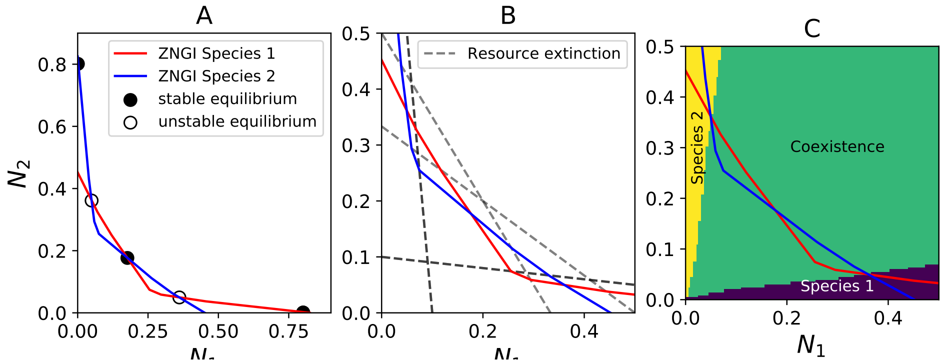

Figure B.3: A: Species competing for 6 resources feature 5 equilibria. Two unstable (empty circle) and three stable. One equilibrium where species coexist (intersection of ZNGI) and each species in monoculture. B: The multiple equilibria can be explained by the different resources. At each equilibria a different set of resources is extinct, such that the species interactions differ. C: Depending on the starting conditions the community will end up in different equilibrium state, where the species either coexist of exclude each other. The invasion growth rates correctly predict the equilibria at the boundaries, not however that the species can coexist.

B.2 Essential resources

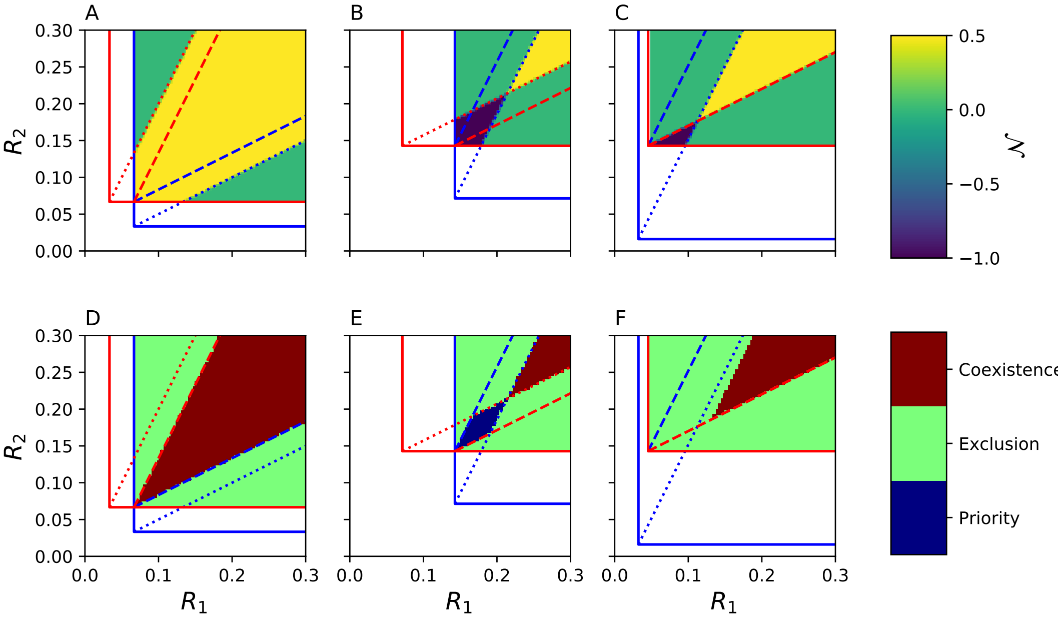

Figure B.4: $\mathcal{N}^A$ and predictions for competitive outcomes for the three qualitatively different cases of competition for essential resources. The upper row reports $\mathcal{N}^A$, the lower row reports the outcome of competition as predicted by the linearisation approach. A,D: In the first case species coexist when the resource supply ratio is within the dashed lines, which is correctly predicted by the linearisation. B,E: In the second case species either competitively exclude each other (resource supply outside of the dashed lines) or have priority effects. However, the linearisation approach does not correctly predict most of the priority effects and even predicts coexistence and positive niche differences. C,F: In the third case the blue species always excludes the red species, independent of the resource supply ratios. However, the linearisation approach predicts coexistence for some of the resource supply ratios.

Letten *et al.* (2017) have shown, that the linearisation of the community model and the actual community model have the same conditions for coexistence. However, both this proof implicitly assumes, that a species is always limited by the same resource independent of species densities. The relaxation of this assumption leads to incorrect predictions about the outcome of competition. There are three qualitatively different ways in which the species can compete for essential resources (Fig. B.4). First, the species may coexist or competitively exclude each other, depending on the resource supply ratios (A). In this case the limiting resource is the same at invasion as when no species are present (intrinsic growth rate), then coexistence is predicted correctly (D, proof see B.5). Second, the species may have priority effects or exclude each other, depending on the resource supply rations (B). In this case the limiting resource can switch, which leads to wrong predictions about coexistence (E). Third, species one excludes the other species, independent of resource supply ratios (C). Again, in this case the limiting resource can switch and coexistence is not predicted correctly (F).

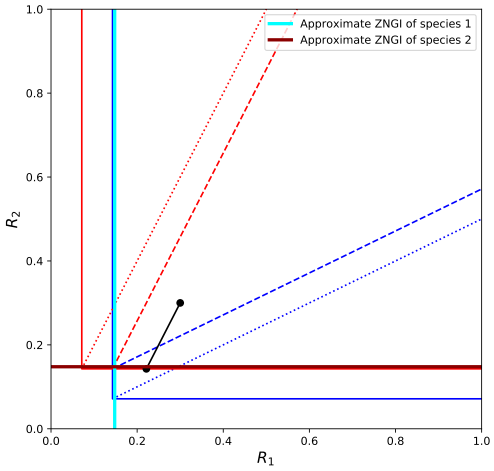

Figure B.5: The linear approximation leads to a linear ZNGI (dark red and cyan), which approximate the real ZNGI (red and blue). The approximated ZNGI assume that the non-limiting resource is never limiting. Which of the two branches from the correct ZNGI are chosen depends on the resource supply rate, more specifically whether the resource supply rate (black dot) is left or right from the dotted blue and red lines. If the species coexist in the real community (resource supply between dashed lines), then the ZNGI are approximated as shown. These ZNGI lead to coexistence, if and only if the resource supply is between the dashed lines, i.e. the linearisation correctly predicts coexistence.

B.3 Maxima and minima of niche differences

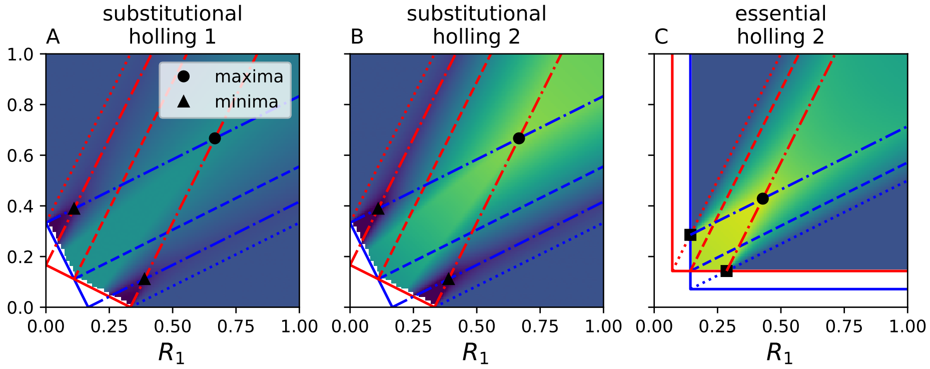

Figure B.6: The maxima and minima of $\mathcal{N}^C$ can be found geometrically by intersecting resource consumption vectors. A,B,C: In the top right region (delimited by the dash dotted lines intersection at the black dot) the invasion growth rates of both species are maximal and constant. Of all the resource supply points within this region the intrinsic growth rates are minimal for both species at the black dot. As niche differences increase with invasion growth rates and decrease with the intrinsic growth rates this is the location where niche differences are maximal. A,B: Competition for substitutional resources features two local minima (one of which is global) and one global maximum. The dash-dotted lines are parallel to the resource consumption vectors of the corresponding colour and intersect the resource axis at the ZNGI. The intersection of two such lines lead to a local maxima (black dot) or minima (black triangle). The minimal of niche differences are located where one species has maximal and the other species has a minimal invasion growth rate. C: Again, the global maxima of $\mathcal{N}^C$ is located at the intersection of two resource consumption vectors (dash-dotted lines). These resource consumption vectors are anchored where the dotted consumption vectors intersect the ZNGI of the other species (black square).

B.4 Comparing methods to compute niche and fitness differences

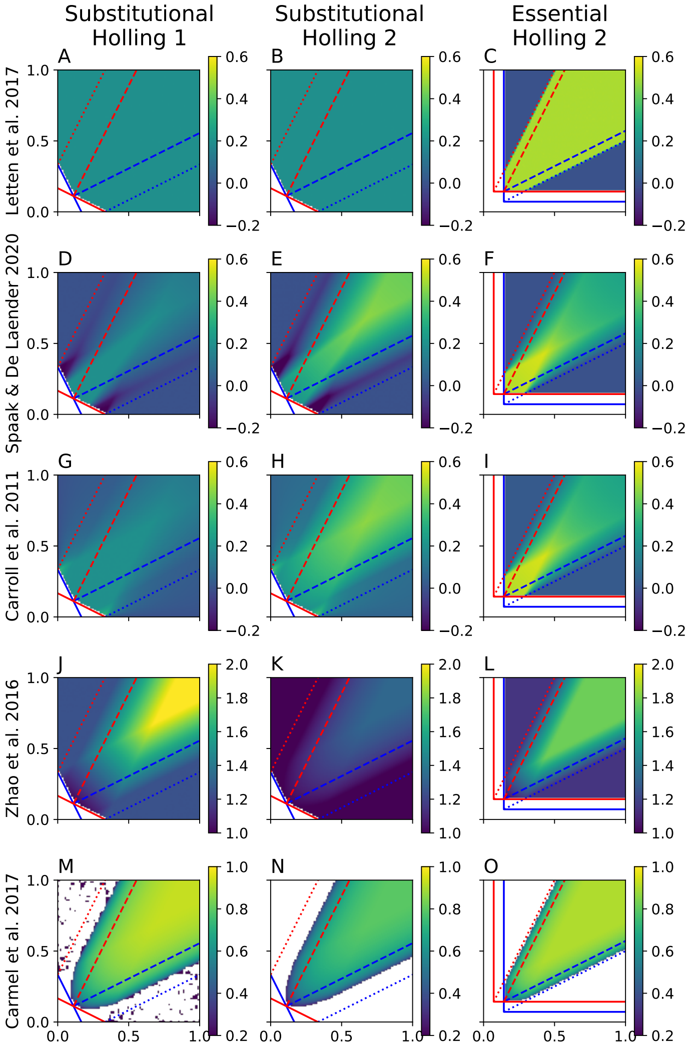

Figure B.7: Niche differences for five different methods (rows) and 3 different models (colums). Spaak & De Laender (2020) is the only method that correctly predicts zero niche differences when species compete only for one resource (outside the dotted lines). The definition of Carmel *et al.* (2017) is not defined for some cases where the species can survive in monoculture (white region). Please note that the color scales differ per method.

There are other methods to compute niche and fitness differences. The most often used definition not investigated in the main text is by Carroll *et al.* (2011). Their method can be understood as a linear approximation of the community model, with $\frac{\alpha_{ij}}{\alpha_{jj}} = \frac{f_i(0,N_j^*)}{f_i(0,0)}$, where $f_i(0, N_j^*)$ is the invasion growth rate and $f_i(0,0)$ is the intrinsic growth rate. Two other methods use the invasion growth rates to define niche and fitness differences. All these methods are based on invasion growth rates, therefore they correctly predict the outcome of competition in the cases analysed, similarly to the method based on the full model. However, all of these methods have non-zero niche differences, when the two species compete for only one resource.

Again other definitions are based specific community models, notably linear community models (see Spaak & De Laender (2020) for a review). We do not review these, as they all require to first fit a linear model which comes with the disadvantages discussed in the main text.

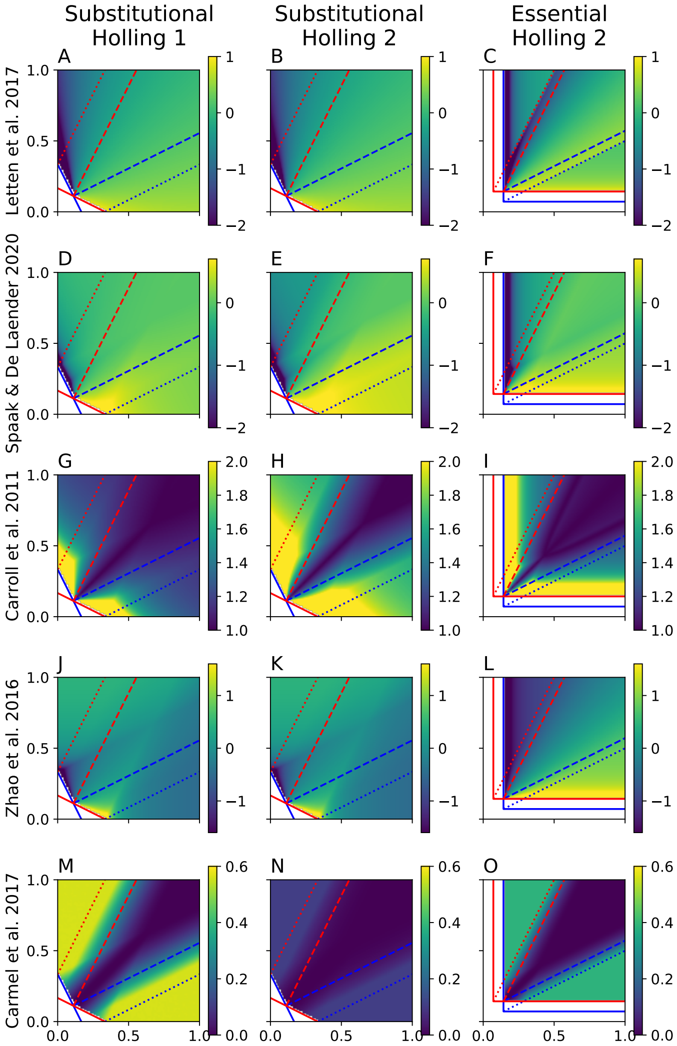

Figure B.8: Fitness differences for five different methods (rows) and 3 different models (colums). The definitions also differ for the interpretation of competitive equivalence. For the definitions Letten *et al.* (2017); Spaak & De Laender (2020); Zhao *et al.* (2016) and Carmel *et al.* (2017) species with equal competitive strength with have zero fitness differences, while for Carroll *et al.* (2011) fitness differences of one imply competitive equality. Please note that the colorscales differ per method.

B.5 The annual plant model

Godoy & Levine (2014) show that niche and fitness differences as defined by them correctly predict coexistence. We show here, that the two methods to compute niche differences agree on when the two species occupy the same niche. Assume $\mathcal{N}^A = 0 \Leftrightarrow \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} = 1$. We can then choose $c_j = \frac{g_i}{g_j}\sqrt{\frac{\alpha_{jj}\alpha_{ij}}{\alpha_{ji}\alpha_{ii}}}$ which results in:

$$\exp(f_i(0,N_j^*)) = (1-g_i)s_i + \frac{\lambda_i g_i}{1+\alpha_{ij}g_jN_j^*} \tag{B.1}$$

$$= (1-g_i)s_i + \frac{\lambda_i g_i}{1+\sqrt{\frac{\alpha_{jj}\alpha_{ii}}{\alpha_{ji}\alpha_{ij}}}\alpha_{ij}g_jN_j^*} \tag{B.2}$$

$$= (1-g_i)s_i + \frac{\lambda_i g_i}{1+\alpha_{ii}\sqrt{\frac{\alpha_{jj}\alpha_{ij}}{\alpha_{ji}\alpha_{ii}}}g_jN_j^*} \tag{B.3}$$

$$= (1-g_i)s_i + \frac{\lambda_i g_i}{1+\alpha_{ii}g_ic_jN_j^*} \tag{B.4}$$

$$= \exp(f_i(c_jN_j^*,0)) \Rightarrow \mathcal{N}^C = 0 \tag{B.5}$$

Conversely, assume that $\mathcal{N}^C = 0$, then we have $f_i(0,N_j^*) = f_i(c_jN_j^*,0) \Leftrightarrow \alpha_{ij}g_jN_j^* = \alpha_{ii}g_ic_jN_j^*$ and similarly $\alpha_{ji}g_iN_i^* = \alpha_{jj}g_jc_iN_i^*$, which leads together with the equation $c_j = c_i^{-1}$ to $\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} = 1$.

B.6 How to compute $\mathcal{N}^C$ and $\mathcal{F}^C$ in resource explicit models

Spaak & De Laender (2020) define niche and fitness differences for a community in which the species growth rates depend directly on the species densities, i.e. $\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, N_j)$. In the resource explicit models the species growth rates do not depend directly on the species densities, but rather on the resources densities and therefore indirectly on the species densities. To compute $\mathcal{N}^C$ and $\mathcal{F}^C$ we have to compute the intrinsic growth rate ($f_i(0,0)$), the invasion growth rate ($f_i(N_j,0)$) and the no-niche growth rate ($f_i(c_jN_j,0)$). The invasion growth rate of the species is computed, when the resident species j is at equilibrium, this implies that the resources are also at equilibrium. Similarly, the intrinsic growth rate is the growth rate when no species has yet consumed any resources, consequently all resources are at carrying capacity (and also at equilibrium). Finally, the no-niche growth rate is the growth rate, when species i is at the converted equilibrium density of species j, therefore the resources are again at equilibrium. That is, to compute $\mathcal{N}^C$ and $\mathcal{F}^C$ we can assume that the resources are at equilibrium. However, we do not assume that the dynamics of the resources are faster than the dynamics of species (time-scale separation), rather all growth rates are evaluated at equilibrium.

We illustrate how to compute $\mathcal{N}^C$ and $\mathcal{F}^C$ for two species competing for substitutable resources with Holling type 2 response functions. First we set the resource densities to equilibrium, i.e. $\frac{dR_l}{dt} = 0 = S_l - R_l - \sum_j u_{lj}N_j$, which leads to $R_l = S_l - \sum_j u_{lj}N_j$. Note this equation holds only for all resources that are not extinct, all other resources have $R_l = 0$, for notational convenience we assume that no resources go extinct. We now compute the equilibrium density of species j:

$$\frac{1}{N_j}dN_jdt = 0 = \frac{\sum_l w_{jl}R_l}{k_j + \sum_l w_{jl}R_l} - m_j \tag{B.6}$$

$$= \frac{\sum_l w_{jl}\left(S_l - u_{lj}N_j\right)}{k_j + \sum_l w_{jl}\left(S_l - u_{lj}N_j\right)} - m_j \tag{B.7}$$

$$m_j\left(k_j + \sum_l w_{jl}\left(S_l - u_{lj}N_j\right)\right) = \sum_l w_{jl}\left(S_l - u_{lj}N_j\right) \tag{B.8}$$

$$m_jk_j + m_j\sum_l w_{jl}S_l - m_j\sum_l w_{jl}u_{lj}N_j = \sum_l w_{jl}S_l - \sum_l w_{jl}u_{lj}N_j \tag{B.9}$$

$$(1-m_j)\sum_l w_{jl}u_{lj}N_j = (1-m_j)\sum_l w_{jl}S_l - m_jk_j \tag{B.10}$$

$$N_j = \frac{\sum_l w_{jl}S_l - \frac{m_jk_j}{1-m_j}}{\sum_l w_{jl}u_{lj}} \tag{B.11}$$

This is of course exactly $\frac{1}{\alpha_{jj}}$ from table 1, as we assumed that no resources go extinct. We can now compute the invasion growth rate of species i with

$$f_i(0,N_j^*) = \frac{\sum_l w_{il}R_l}{k_l + \sum_l w_{il}R_l} - m_i \tag{B.12}$$

$$= \frac{\sum_l w_{il}\left(S_l - u_{lj}N_j^*\right)}{k_l + \sum_l w_{il}\left(S_l - u_{lj}N_j^*\right)} - m_i \tag{B.13}$$

$$= \frac{\sum_l w_{il}\left(S_l - u_{lj}\frac{\sum_l w_{jl}S_l - \frac{m_jk_j}{1-m_j}}{\sum_l w_{jl}u_{lj}}\right)}{k_l + \sum_l w_{il}\left(S_l - u_{lj}\frac{\sum_l w_{jl}S_l - \frac{m_jk_j}{1-m_j}}{\sum_l w_{jl}u_{lj}}\right)} - m_i \tag{B.14}$$

The intrinsic growth rate is given by

$$f_i(0,0) = \frac{\sum_l w_{il}S_l}{k_i + \sum_l w_{il}S_l} - m_i \tag{B.15}$$

Again, this is identical to r_i from table 1.

Finally, to compute the no-niche growth rate we have to solve the following equation for c_j:

$$\frac{\frac{\sum_l w_{il}\left(S_l-u_{lj}N_j^*\right)}{k_l+\sum_l w_{il}\left(S_l-u_{lj}N_j^*\right)}-m_i-\left(\frac{\sum_l w_{il}\left(S_l-u_{lj}c_jN_j^*\right)}{k_l+\sum_l w_{il}\left(S_l-u_{lj}c_jN_j^*\right)}-m_i\right)}{\frac{\sum_l w_{il}(S_l)}{k_l+\sum_l w_{il}(S_l)}-m_i-\left(\frac{\sum_l w_{il}\left(S_l-u_{lj}c_jN_j^*\right)}{k_l+\sum_l w_{il}\left(S_l-u_{lj}c_jN_j^*\right)}-m_i\right)}= \tag{B.16}$$

$$\frac{\frac{\sum_l w_{jl}\left(S_l-u_{li}N_i^*\right)}{k_l+\sum_l w_{jl}\left(S_l-u_{li}N_i^*\right)}-m_j-\left(\frac{\sum_l w_{jl}\left(S_l-u_{li}c_iN_i^*\right)}{k_l+\sum_l w_{jl}\left(S_l-u_{li}c_iN_i^*\right)}-m_j\right)}{\frac{\sum_l w_{jl}(S_l)}{k_l+\sum_l w_{jl}(S_l)}-m_j-\left(\frac{\sum_l w_{jl}\left(S_l-u_{li}c_iN_i^*\right)}{k_l+\sum_l w_{jl}\left(S_l-u_{li}c_iN_i^*\right)}-m_j\right)} \tag{B.17}$$

While this equation may look very daunting, it's actually reasonably simple. $c_j = \frac{1}{c_i}$ is the only variable, everything else are parameters. The equation cannot be solved analytically, but very easily with numerical methods.

Appendix C

Appendix for chapter 4

C.1 Derivation of $\mathcal{N}$ and $\mathcal{F}$ in multispecies communities

For a multispecies community we define

$$\mathcal{N}_i = \frac{f_i(0, \boldsymbol{N}^{-i,*}) - f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \boldsymbol{0})}{f_i(0, \boldsymbol{0}) - f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \boldsymbol{0})} \tag{C.1}$$

$$\mathcal{F}_i = \frac{f_i(\sum_{j\neq i} c_{ij} N_j^{-i,*}, \boldsymbol{0})}{f_i(0, \boldsymbol{0})} \tag{C.2}$$

, where f_i is the per capita growth rate of species i (i.e. $f_i(N_i, \boldsymbol{N}^{-i}) = \frac{1}{N_i}\frac{dN_i}{dt}$. The first argument of f_i, N_i, is the density of the focal species i; the second argument ($\boldsymbol{N}^{-i}$) is a vector of length $n-1$ containing the densities of the $n-1$ non-focal species. $\boldsymbol{N}^{-i,*}$ is the equilibrium density of all non-focal species in the absence of species i. $f_i(0, \boldsymbol{N}^{-i,*})$ is the invasion growth rate, $f_i(0, \boldsymbol{0})$ is the intrinsic growth rate and $f_i(\sum_{i\neq j} c_{ij} N_j^{-i,*}, \boldsymbol{0})$ is the no-niche growth rate (Spaak & De Laender, 2020). The no-niche growth rate can be computed with the c_{ij}, the conversion factor of species j to species i. These factors convert species densities such that species i and j have the same total influence on limiting factor (see fig. 4.1; for details see Spaak & De Laender (2020)). Mathematically, these are defined as the solution of the equations

$$c_{ij} = \frac{1}{c_{ji}} \tag{C.3}$$

$$\frac{f_i(0, \boldsymbol{N}^{-\boldsymbol{i},*}) - f_i(c_{ij}N_j^{-i,*}, \boldsymbol{N}_{-\boldsymbol{j}}^{-\boldsymbol{i},*})}{f_i(0, \boldsymbol{N}_{-\boldsymbol{j}}^{-\boldsymbol{i},*}) - f_i(c_{ij}N_j^{-i,*}, \boldsymbol{N}_{-\boldsymbol{j}}^{-\boldsymbol{i},*})} = \frac{f_j(0, \boldsymbol{N}^{-\boldsymbol{j},*}) - f_j(c_{ji}N_i^{-j,*}, \boldsymbol{N}_{-\boldsymbol{i}}^{-\boldsymbol{j},*})}{f_j(0, \boldsymbol{N}_{-\boldsymbol{i}}^{-\boldsymbol{j},*}) - f_j(c_{ji}N_i^{-j,*}, \boldsymbol{N}_{-\boldsymbol{i}}^{-\boldsymbol{j},*})} \tag{C.4}$$

where $\boldsymbol{N}_{-\boldsymbol{j}}^{-\boldsymbol{i},*}$ is the vector $\boldsymbol{N}^{-\boldsymbol{i},*}$ with entry j set to 0. The first equation ensures that converting species i to j is the inverse action to converting species j to species i. The second equation expresses that the two species have the same total converted consumption (Fig. 4.1C): The numerator of the left hand side compares two growth rates of species i with identical converted densities but different frequencies of species i. It therefore assesses the effect of interspecific interactions on species i's growth. The denominator of the left hand side compares two growth rates of species i with identical frequencies of species i, but different densities of species i. It therefore assesses the effect of intraspecific interactions. Numerator and denominator of the right hand side have identical interpretations but for species j. Equation C.4 thus expresses the condition under which the two species have the same response to competition, which can be interpreted as the two species having the same total consumption rates. Spaak & De Laender (2020) show that these equations have a unique solution for the generalised Lotka-Voltera model.

C.1.1 First-order interactions

In this section we assume that higher order interactions are absent, i.e. $\beta_{ijk} = \gamma_{ijkl} = 0$. This case is equivalent to the Lotka-Volterra equations. This case has already been solved in the appendix of Spaak & De Laender (2020), we merely repeat their findings here. The niche difference between species i and j in the multispecies community is

$$\frac{f_i(0,\boldsymbol{N}^{-i,*}) - f_i(c_{ij}N_j^{-i,*},\boldsymbol{N}_{-j}^{-i,*})}{f_i(0,\boldsymbol{0}) - f_i(c_{ij}N_j^{-i,*},\boldsymbol{N}_{-j}^{-i,*})} = \tag{C.5}$$

$$= \frac{\left(1-\sum_{k\neq i}\alpha_{ik}N_k^{-i,*}\right) - \left(1-\sum_{k\neq i,j}\alpha_{ik}N_k^{-i,*} - \alpha_{ii}c_{ij}N_j^{-i,*}\right)}{\left(1-\sum_{k\neq i,j}\alpha_{ik}N_k^{-i,*}\right) - \left(1-\sum_{k\neq i,j}\alpha_{ik}N_k^{-i,*} - \alpha_{ii}c_{ij}N_j^{-i,*}\right)} \tag{C.6}$$

$$= \frac{\left(c_{ij}\alpha_{ii} - \alpha_{ij}\right)N_j^{-i,*}}{c_{ij}\alpha_{ii}N_j^{-i,*}} \tag{C.7}$$

$$= 1 - \frac{\alpha_{ij}}{c_{ij}\alpha_{ii}} \tag{C.8}$$

The absence of species j in $\boldsymbol{N}_{-j}^{-i,*}$ is handled by omitting this index in the summation. By solving $|1-\frac{\alpha_{ij}}{c_{ij}\alpha_{ii}}| = |1-\frac{\alpha_{ji}}{c_{ij}^{-1}\alpha_{jj}}|$ we get $c_{ij} = \sqrt{\left|\frac{\alpha_{jj}\alpha_{ij}}{\alpha_{ii}\alpha_{ji}}\right|}$. c_{ij} is set to 0 if this value is not defined (i.e. $\alpha_{ji} = 0$) (Spaak & De Laender, 2020). For a two species community we therefore get

$$1-\mathcal{N}_{ij} = sign(a_{ij})\sqrt{\left|\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}\right|} \tag{C.9}$$

$$1-\mathcal{F}_{ij} = \sqrt{\left|\frac{\alpha_{ii}\alpha_{ij}}{\alpha_{jj}\alpha ji}\right|} \tag{C.10}$$

With this we can show that $1-\mathcal{N}_i$ is a weighted average and $1-\mathcal{F}_i$ is a weighted sum:

$$1-\mathcal{N}_i = \frac{1-\left(1-\sum_{j\neq i}\alpha_{ij}N_j^{-i,*}\right)}{1-\left(1-\sum_{j\neq i}c_{ij}\alpha_{ii}N_j^{-i,*}\right)} \tag{C.11}$$

$$= \frac{\sum_{j\neq i}\frac{\alpha_{ij}}{a_{ii}}N_j^{-i,*}}{\sum_{j\neq i}c_{ij}N_j^{-i,*}} \tag{C.12}$$

$$= \frac{\sum_{j\neq i}1-\mathcal{N}_{ij}c_{ij}N_j^{-i,*}}{\sum_{j\neq i}c_{ij}N_j^{-i,*}} \tag{C.13}$$

$$1-\mathcal{F}_i = 1-\left(1-\sum_{j\neq i} c_{ij}\alpha_{ii}N_j^{-i^*}\right) \tag{C.14}$$

$$= \sum_{j\neq i}\sqrt{\left|\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{ji}\alpha_{jj}}\right|}\alpha_{jj}N_j^{-i,*} \tag{C.15}$$

$$= \sum_{j\neq i} 1-\mathcal{F}_{ij}\frac{N_j^{-i,*}}{N_j^*} \tag{C.16}$$

Which proves the equations 6 and 7 in the main-text.

To obtain the case where $\alpha_{ij}=\bar{\alpha}$ we remark that $c_{ij}=1$, $\mathcal{N}_{ij}=\bar{\alpha}$, $\mathcal{F}_{ij}=0$, $N_j^{-i,*}=\frac{1}{1+(n-2)\bar{\alpha}}$ and N_j^*. This leads to

$$\mathcal{N}_i = 1-\frac{\sum_{j\neq i}(1-\mathcal{N}_{ij})c_{ij}N_j^{-i,*}}{\sum_{j\neq i}c_{ij}N_j^{-i,*}} \tag{C.17}$$

$$= 1-\frac{\sum_{j\neq i}(1-\bar{\alpha})\frac{1}{1+(n-2)\bar{\alpha}}}{\sum_{j\neq i}\frac{1}{1+(n-2)\bar{\alpha}}} \tag{C.18}$$

$$= 1-\bar{\alpha} \tag{C.19}$$

$$\mathcal{F}_i = 1-\sum_{j\neq i}(1-\mathcal{F}_{ij})\frac{N_j^{-i,*}}{N_j^*} \tag{C.20}$$

$$= 1-\sum_{j\neq i}(1-0)\frac{\frac{1}{1+(n-2)\bar{\alpha}}}{1} \tag{C.21}$$

$$= 1-\frac{n-1}{1+(n-2)\bar{\alpha}} \tag{C.22}$$

C.1.2 Higher-order interactions

We assume $\alpha_{ij}=\bar{\alpha}$ and $\beta_{ijk}=\bar{\beta}$ and omit the overbars in this subsection for notational simplicity. By symmetry we have $N_j^{-i,*}=N_k^{-i,*}=N^{-i,*}$ and $c_{ij}=c_{ji}=1$.

$$\mathcal{N}_i^m = \frac{r_i\left(1-\sum_j \alpha N^{-i,*}\left(1+\sum_k \beta N^{-i,*}\right)\right) - r_i\left(1-\sum_j N^{-i,*}\left(1+\beta\sum_k N^{-i,*}\right)\right)}{r_i - r_i\left(1-\sum_j N^{-i,*}\left(1+\beta\sum_k N^{-i,*}\right)\right)} \tag{C.23}$$

$$= \frac{(1-\alpha)(n-1)N^{-i,*}(1+\beta(n-1)N^{-i,*})}{(n-1)N^{-i,*}(1+\beta(n-1)N^{-i,*})} \tag{C.24}$$

$$= 1-\alpha \tag{C.25}$$

To compute $\mathcal{F}_i^m$ we first make some observations about the equilibrium density $N^{-i,*}$:

$$0 = 1 - \left(N^{-i,*} + \alpha(n-2)N^{-i,*}\right)\left(1+\beta(n-1)N^{-i,*}\right) \tag{C.26}$$

$$1 = \left(N^{-i,*} + \alpha(n-2)N^{-i,*}\right)\left(1+\beta(n-1)N^{-i,*}\right) \tag{C.27}$$

$$\frac{1}{N^{-i,*} + \alpha(n-2)N^{-i,*}} = 1+\beta(n-1)N^{-i,*} \tag{C.28}$$

$$\mathcal{F}_i^m = 1-(n-1)N^{-i,*}(1+\beta(n-1)N^{-i,*}) \tag{C.29}$$

$$= 1 - \frac{(n-1)N^{-i,*}}{N^{-i,*} + \alpha(n-2)N^{-i,*}} \tag{C.30}$$

$$= 1 - \frac{n-1}{1-(n-2)\alpha} \tag{C.31}$$

Higher order interactions therefore do not affect $\mathcal{N}$ and $\mathcal{F}$ on average.

C.1.3 Indirect effects

To investigate complexity (iv) we removed indirect effects. Indirect effects are defined as a third species k affecting densities of the non-focal species j, which affects the effect of species j on the focal species i. To remove these indirect effects we set $N_j^{-i,*} = N_j^*$, i.e. a species k does not affect the density of species j. Note however, that species k can still affect species i directly via α_{ik} or via higher-order effects (e.g. β_{ijk}).

$$\mathcal{F}_i^m = 1 - \sum_{\alpha_{ij}\neq 0} (1 - \mathcal{F}_{ij}) \frac{N_j^{-i,*}}{N_j^*} \tag{C.32}$$

$$= 1 - \sum_{\alpha_{ij}\neq 0} (1 - \mathcal{F}_{ij}) \frac{N_j^*}{N_j^*} \tag{C.33}$$

$$= 1 - \sum_{\alpha_{ij}\neq 0} (1 - \mathcal{F}_{ij}) \tag{C.34}$$

$$\mathcal{N}_i^m = \frac{\sum_{\alpha_{ij}\neq 0}(1 - \mathcal{N}_{ij}) N_j^{-i,*}}{\sum_{\alpha_{ij}\neq 0} c_{ij} N_j^{-i,*}} \tag{C.35}$$

$$= \frac{\sum_{\alpha_{ij}\neq 0}(1 - \mathcal{N}_{ij}) c_{ij} N_j^*}{\sum_{\alpha_{ij}\neq 0} c_{ij} N_j^*} \tag{C.36}$$

$\mathcal{F}_i$ changes from a saturating to a linear response in species richness, i.e. $\mathcal{F}_i \approx 1 - (n-1)$ on average. Conversely, removing indirect effects will not change $\mathcal{N}_i$ on average. Thus, indirect effects will mostly not change the response of $\mathcal{N}_i$ to species richness. This yields an important result: Indirect effects are purely equalizing as they do not change niche differences, and thus promote coexistence.

C.2 Simulations

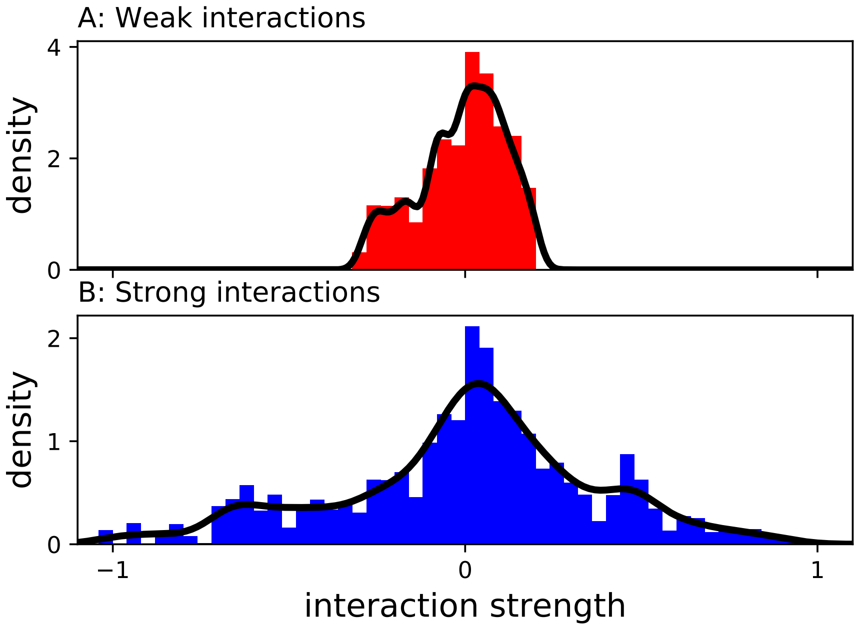

Figure C.1: Interaction strength distributions for weak (A) and strong (B) first-order interactions. Histogram shows the distribution of the interaction strength of empirical communities that coexist. We fit a guassian kernel density distribution (black line) to the distribution of the interaction strength of empicial communities that coexist (histogram). We removed outliers, defined as interaction strength that were below $Q_1 - 1.5(Q_3 - Q_1)$ or above $Q_3 + 1.5(Q_3 - Q_1)$, where Q_1 and Q_3 are the first and third quartile. For weak interaction strength we only retained interaction strength within the first and third quartile.

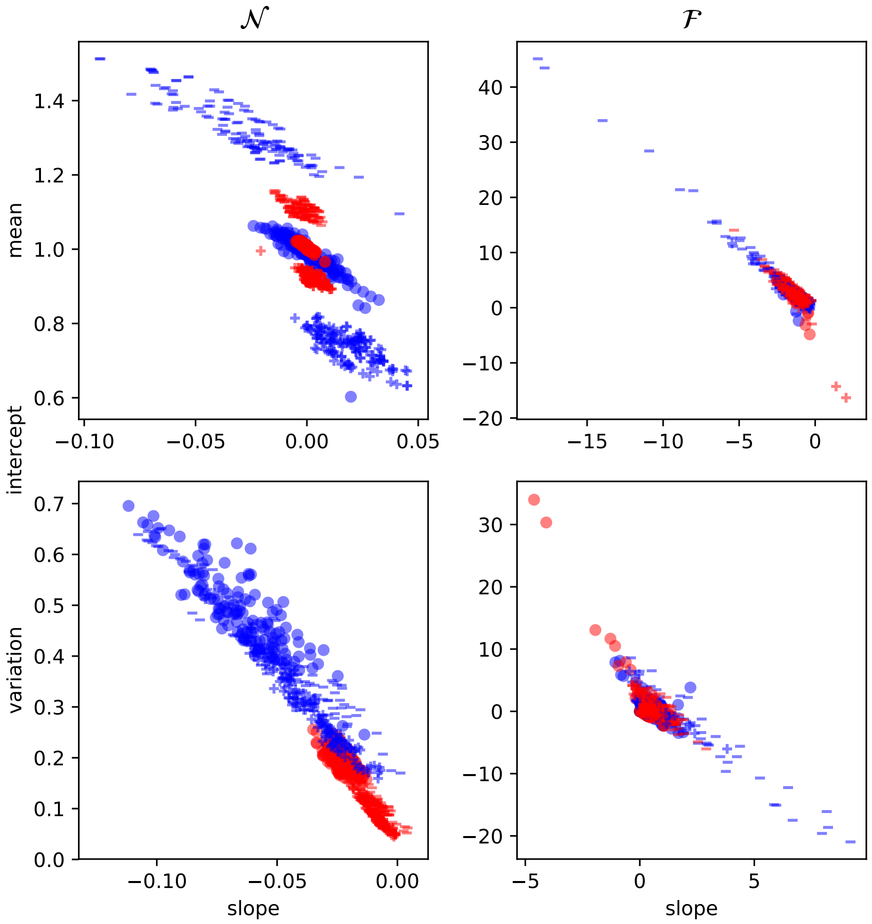

Figure C.2: Effects of species richness on $\mathcal{N}$ and $\mathcal{F}$ (top row) and on variation of $\mathcal{N}$ and $\mathcal{F}$ (bottom row) per factor combination of the full-factorial design. For each factor combination we fit a linear regression of the response variable as a function of species richness. X-axis correspond to the slope, y-axis correspond to the intercept of the linear regression. Color codes the strength of first-order interaction: red: weak, blue: strong. Shape codes the type of first-order interactions: minus: facilitation, plus: competition, dot: both. The first-order interaction affects the intercept of $\mathcal{N}$ and variation of $\mathcal{N}$ most. Variation of $\mathcal{N}$ decreased for almost all factor combinations. $\mathcal{F}$ decreased in almost all factor combination.

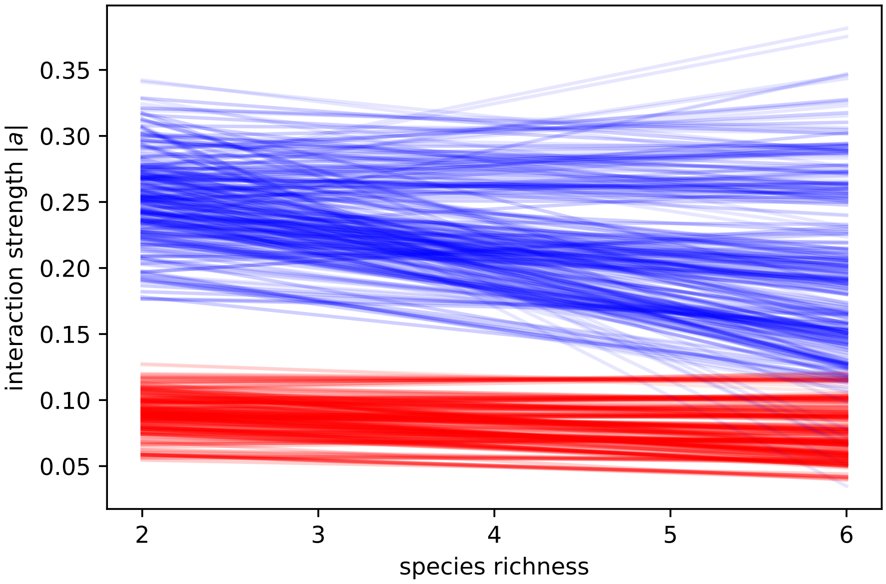

Figure C.3: Effects of species richness on absolute interaction strength. The y-axis shows the mean of the absolute interspecific-interaction strength. Each line is a linear fit of species richness versus interaction strength in one of the full-factorial settings. Species richness affects interaction strength in communities with strong first-order interactions (blue lines) mostly negatively. Species richness has a minor effect on interaction strength in communities with weak first-order interactions (red lines).

	ND slope	ND var slope	FD slope	FD var slope
ord1: negative	[-0.014; 0.003]	[-0.027; -0.005]	[-3.003; -0.915]	[0.001; 1.446]
ord1: unrestricted	[-0.004; 0.003]	[-0.031; -0.016]	[-1.808; -0.607]	[-0.43; 0.772]
ord1: positive	[-0.002; 0.009]	[-0.016; -0.002]	[-1.978; -0.577]	[-0.125; 0.72]
ord2: negative	[-0.014; 0.008]	[-0.029; -0.004]	[-2.11; -0.817]	[-0.05; 0.889]
ord2: absent	[-0.01; 0.008]	[-0.029; -0.004]	[-2.379; -0.707]	[-0.091; 1.438]
ord2: positive	[-0.014; 0.007]	[-0.029; -0.007]	[-2.837; -0.746]	[-0.942; 1.276]
ord2: unrestricted	[-0.005; 0.003]	[-0.025; -0.002]	[-2.192; -0.564]	[0.02; 0.921]
ord3: absent	[-0.01; 0.008]	[-0.026; -0.005]	[-2.688; -0.588]	[-0.199; 1.133]
ord3: present	[-0.013; 0.007]	[-0.029; -0.003]	[-2.532; -0.692]	[0.097; 1.253]
con: high	[-0.014; 0.009]	[-0.029; -0.005]	[-2.521; -0.563]	[-0.113; 1.251]
con: middle	[-0.006; 0.003]	[-0.027; -0.002]	[-2.929; -0.709]	[0.06; 1.32]
con: low	[-0.008; 0.005]	[-0.027; -0.005]	[-2.421; -0.751]	[-0.257; 0.965]
cor: negative	[-0.009; 0.006]	[-0.029; -0.001]	[-2.791; -0.737]	[0.077; 1.25]
cor: positive	[-0.011; 0.008]	[-0.025; -0.005]	[-2.659; -0.73]	[-0.316; 1.38]
cor: none	[-0.014; 0.009]	[-0.029; -0.009]	[-2.218; -0.588]	[-0.164; 1.001]
indirect: absent	[-0.01; 0.008]	[-0.028; -0.004]	[-2.742; -0.633]	[-0.036; 1.323]
indirect: present	[-0.01; 0.007]	[-0.028; -0.004]	[-2.325; -0.627]	[-0.108; 1.009]

Table C.1: For each factor level (row names) we show the 5% and the 95% percentiles for the slopes of $\mathcal{N}_i$, $\mathcal{F}_i$ and their interquartile range.

C.3 Literature Data

	2	3	4	5	6	7	8	9	Total
Original matrices	0	8	13	1	5	3	0	3	33
Subcommunities	358	527	576	472	278	111	27	3	2544
int. matrix"	356	517	557	455	271	110	27	3	2296
NFD computed	356	371	140	45	8	0	0	0	920
coexistence	290	270	142	55	11	0	0	0	768
comp. exclusion	66	247	415	400	260	110	27	3	1528
no invasion analysis	0	8	23	12	3	0	0	0	46
invasion wrong	0	3	0	0	0	0	0	0	3
NFD coexistence	290	262	119	43	8	0	0	0	722
NFD comp. excl	66	109	21	2	0	0	0	0	198

Table C.2: Number of communities per species richness (top row). *Original matrices*: Number of different communities found in the literature. *Subcommunities*: Number of subcommunities generated out of all matrices. *int. matrix*: Number of communities in which all interaction strength are present. *NFD computed*: Number of communities for which we were able to compute $\mathcal{N}$ and $\mathcal{F}$. *coexistence*: Number of communities with a stable point equilibrium. *comp. exclustion*: Number of communities with no stable point equilibrium. *no invasion analysis*: Number of communities in which at least one subcommunity did not have a stable equilibrium, preventing invasion analysis. *invasion wrong*: Number of communities in which invasion as predicted by invasion analysis did not agree with coexistence as defined by stable point equilibrium. All three communities stem from the same original matrix. The species facilitate each other, such that invasion is positive, however densities explode to infinity. *NFD coexistence*: Number of communities in which $\mathcal{N}$ and $\mathcal{F}$ predict coexistence. *NFD comp. excl*: Number of communities in which $\mathcal{N}$ and $\mathcal{F}$ predict competitive exclusion.

C.4 Definition by Carroll et al.

Carroll *et al.* (2011) define $\mathcal{N}$ and $\mathcal{F}$ as:

$$S_i = \frac{f_i(0,\mathbf{0}) - f_i(0,\boldsymbol{N}^{-i,*})}{f_i(0,\mathbf{0})} \tag{C.37}$$

$$\mathcal{N}^c = 1 - \exp\left(\text{mean}\left(\log(S_i)\right)\right) \tag{C.38}$$

$$\mathcal{F}^c = \exp\left(\text{var}\left(\log(S_i)\right)\right) \tag{C.39}$$

S_i is the sensitivity of a species to competition. $\mathcal{N}^c$ and $\mathcal{F}^c$ (superscript c for definition of Carroll *et al.* (2011)) are the geometric mean and the geometric variance of the sensitivities S_i.

For simplicity, we assume $\alpha_{ij} = \bar{\alpha}$ and no higher order interactions. With this assumptions, we get $N_j^{-i,*} = N_k^{-i,*} = \frac{1}{1+(n-2)\bar{\alpha}}$.

$$S_i = \frac{1 - (1 - \sum_{j\neq i} \bar{\alpha}\frac{1}{1+(n-2)\bar{\alpha}})}{1} \tag{C.40}$$

$$= \frac{\bar{\alpha}(n-1)}{1+\bar{\alpha}(n-2)} \tag{C.41}$$

$$\mathcal{N}^c = 1 - \frac{\bar{\alpha}(n-1)}{1+\bar{\alpha}(n-2)} \tag{C.42}$$

$$= \frac{1+\bar{\alpha}(n-2) - \bar{\alpha}(n-1)}{1+\bar{\alpha}(n-2)} \tag{C.43}$$

$$= \frac{1-\alpha}{1+\bar{\alpha}(n-2)} \tag{C.44}$$

$$\mathcal{F}^c = 1 \tag{C.45}$$

Hence, indeed $\mathcal{F}^c$ is independent of species richness, and $\mathcal{N}^c$ is approaches 0 with increasing species richness.

Appendix D

Appendix for chapter 5

D.1 Spectrum model

The equation given by Stomp *et al.* (2004) is equivalent to:

$$
\begin{aligned}
\frac{dN_s}{dt} &= \frac{\phi_s}{z_m} \int_0^{z_m} \int_{400}^{700} k_s(\lambda) I_\lambda(z) d\lambda\, dz - l_s && \text{(D.1)} \\
&= \frac{\phi_s}{z_m} \int_{400}^{700} \int_0^{z_m} k_s(\lambda) I_\lambda(z) dz\, d\lambda - l_s && \text{(D.2)} \\
&= \frac{\phi_s}{z_m} \int_{400}^{700} k_s(\lambda) \int_0^{z_m} I_\lambda(z) dz\, d\lambda - l_s && \text{(D.3)} \\
&= \frac{\phi_s}{z_m} \int_{400}^{700} k_s(\lambda) \int_0^{z_m} I_{in}(\lambda) e^{-z\left(\sum_i \frac{N_i}{z_m} k_i(\lambda) + k_{BG}\right)} dz\, d\lambda - l_s && \text{(D.4)} \\
&= \frac{\phi_s}{z_m} \int_{400}^{700} k_s(\lambda) I_{in}(\lambda) \left[\frac{e^{-z\left(\sum_i \frac{N_i}{z_m} k_i(\lambda) + k_{BG}\right)}}{-\left(\sum_i \frac{N_i}{z_m} k_i(\lambda) + k_{BG}\right)} \right]_0^{z_m} d\lambda - l_s && \text{(D.5)} \\
&= \phi_s \int_{400}^{700} \frac{k_s(\lambda) I_{in}(\lambda) \left(1 - e^{-\left(\sum_i N_i k_i(\lambda) + z_m k_{BG}\right)}\right)}{\sum_i N_i k_i(\lambda) + z_m k_{BG}} d\lambda - l_s && \text{(D.6)} \\
&= \phi_s \int_{400}^{700} \frac{k_s(\lambda)}{\text{abs}(\lambda)} \cdot I_{in}(\lambda) \left(1 - e^{-\text{abs}(\lambda)}\right) d\lambda - l_s && \text{(D.7)}
\end{aligned}
$$

Where we introduced the species independent variable $\text{abs}(\lambda) = \sum_i N_i k_i(\lambda) + z_m k_{BG}$ for convenience.

D.2 Pigment table

Pigment	Chl a	Chl b	Chl c	Beta Carotene	Peridinin	Fucoxanthin	PCB	PEB	PUB
Heterokontaphyta 1	1								
Heterokontaphyta 2	1		0.2	0.3					
Heterokontaphyta 3	1		0.2	0.3		0.5			
Haptophyta	1		0.2	0.3		0.5			
Prochlorophyta	1	0.2		0.3					
Euglenophyta	1	0.2		0.3					
Chlorarachniophyta	1	0.2							
Chlorophyta	1	0.2		0.3					
Dinophyta I	1		0.2	0.3	0.5				
Glaucophyta	1			0.3			1		
Rhodophyta	1			0.3			0.25	1	
Cryptophyta	1		0.2				0.25	1	
Cyanophyta 1	1						1		
Cyanophyta 2	1						0.25	1	
Cyanophyta 3	1						0.25	0.25	1

Table D.1: Abberations for pigments: Chl: Chlorophyll, PCB: Phycocyanobilin, PEB: Pyhcoerithrobilin, PUB: Phycourobilin. Shown are only the main pigments according to Van Den Hoek *et al.* (1995) and Six *et al.* (2007). The concentrations of the pigments are taken from Bricaud *et al.* (2004).

D.3 Additional simulations

For the simulation chosen in the main text we took quite strong assumptions, which will potentially not hold in nature. We made a large number of different simulations, none of which changed the general result obtained that trait richness hardly increases species richness. Additionally in all cases the positive effects of trait richness on ecosystem function were more pronounced for short term experiments, in which hardly any species went extinct, than for long term experiments.

These simulations included slight variation of pigment absorption spectra per species, back ground absorption and different fluctuations of incoming light. As an additional example we show the case where the pigment absorption spectra varied up to 5% between species and the background absorption resembles that of a coastal region Stomp *et al.* (2007b) with and without fluctuation of incoming light.

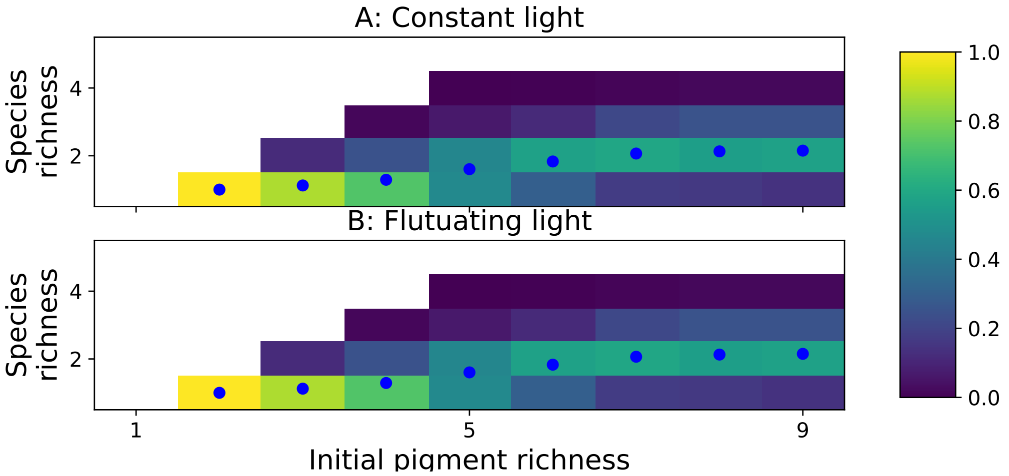

Figure D.1: Final species richness depends only weakly on the initial number of pigments at constant (A) and fluctuating (B) incoming light. Colours denote the probability associated with these species richness levels. Blue dots show the average of the final speices richness. In this simulation we included a background absorption of a coastal region Stomp *et al.* (2007b). Furthermore the interspecific variation of the absorption spectra of the pigment was assumed to be 5%.

D.4 Selection and complementarity

Most species have few different pigments (≤ 3) (See table D.1), hence a community with high initial pigment richness is likely to also have high initial species richness. High initial species richness, however, implies higher probability of having a highly productive species present in the ecosystem. We compute selection, complementarity and relative yield total as described in Hector & Loreau (2001).

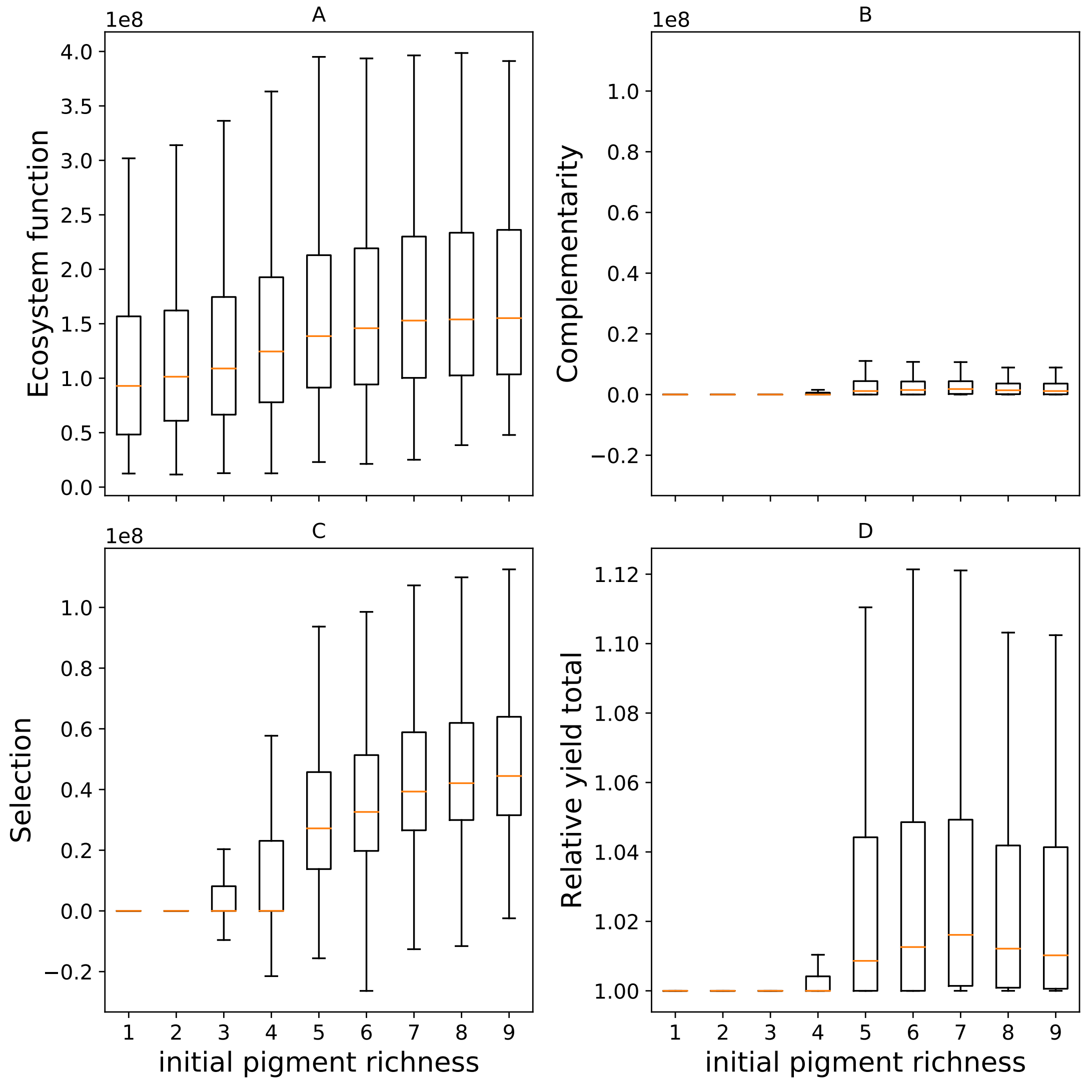

Figure D.2: The positive effect of pigment richness on ecosystem function (A) can be decomposed into complementarity, which is associated with resource partitioning, (B) and selection effect, which is associated with dominance of productive species (C). Initial pigment richness increases both, complementarity and selection effect, however, the selection effect is an order or magnitude stronger than the complementarity effect. D: Initial pigment richness increases relative total yield by 1-2%, which should be considered as minor. That is communities with high pigment richness do not yield much more, than the most productive monoculture species. Shown are 5%, 25%, 50%, 75% and 95% percentiles.

Appendix E

Appendix for chapter 7

E.1 Predator and mutualist communities

I adjusted the community models from Chesson & Kuang (2008) and Johnson & Bronstein (2019) such that they are more similar. The community model for mutualists is:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_l w_{il} R_l + \sum_j \frac{b_{ij} M_j}{1 + \sum_k v_{jk} N_k} - d_i \tag{E.1}$$

$$\frac{1}{M_j}\frac{dM_j}{dt} = \sum_k \frac{a_{jk} N_k}{1 + \sum_k v_{jk} N_k} - \delta_j - M_j \tag{E.2}$$

$$\frac{dR_l}{dt} = S_l - R_l \sum_k c_{lk} N_k R_l \tag{E.3}$$

where N_i is the density of the species i, w_{il} is the conversion efficiency, R_l is the density of resource l, b_{ij} is the service efficiency at which species i profits from interactions with mutualist j, M_j is the density of mutualist j, v_{jk} is the time mutualist j needs to serve species k and d_i is the mortality rate of species i. a_{jk} is the service reward of mutualist j for interacting with species k and δ_j is the mortality rate of mutualist j. Finally, S_l is the resource supply rate of resource l and $c_l k$ is the consumption rate of species k. The community model for predators is

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_l w_{il}R_l - \sum_j b_{ij}P_j - d_i \tag{E.4}$$

$$\frac{1}{P_j}\frac{dP_j}{dt} = \sum_k a_{jk}N_k - \delta_j - P_j \tag{E.5}$$

$$\frac{dR_l}{dt} = S_l - R_l - \sum_k c_{lk}N_kR_l \tag{E.6}$$

where b_{ij} is the consumption rate of predator j and a_{jk} is the conversion efficiency of predator j. For the simulations all parameters where chosen identical for both communities, that is differences between the communities arise from the differences in species interactions and not from differences in community parameters.

To compute niche and fitness differences for only the top level or only the middle trophic level the densities of the other species were set to equilibrium, where the equilibrium depended on the densities of the focal trophic level. This is mathematically equivalent to assuming a time separation between the different trophic levels. However, it does not assume an actual time separation, rather niche and fitness differences are only computed at equilibrium densities, such that all non-focal species are at equilibrium.

E.2 Resource competition trait distribution

Similar to the methods used in chapter 5 I created a community model in which phytoplankton species compete for the essential resources phosphor and nitrogen. The species per capita growth rates are given by

$$\frac{1}{N_i}\frac{dN_i}{dt} = \min_l\left(\frac{w_{il}R_l}{k_{il}+R_l}\right) - l \tag{E.7}$$

$$\frac{dR_l}{dt} = l(S_l - R_l) - \sum_k c_{lk}N_kR_l \tag{E.8}$$

, where N_i is the density of species i, R_l is the density of phosphorus or nitrogen, w_{il} is the maximal growth rate, k_{il} is the half saturation constant, l is the dilution rate, S_l is the resource supply rate and c_{lk} is the resource uptake rate. The species parameter were drawn from a Gaussian kernel distribution fitted to the empirical data from Edwards *et al.* (2015) (see Figure E.1). The other parameters were uniformly distributed ($l \in [0.003, 0.015]h^-1$ see chapter

5, $S_N \in [1.5,3] \mu mol\ L^{-1}$ (Primeau *et al.*, 2013), $S_P \in [15,30] \mu mol\ L^{-1}$(Pillai *et al.*, 2011)).

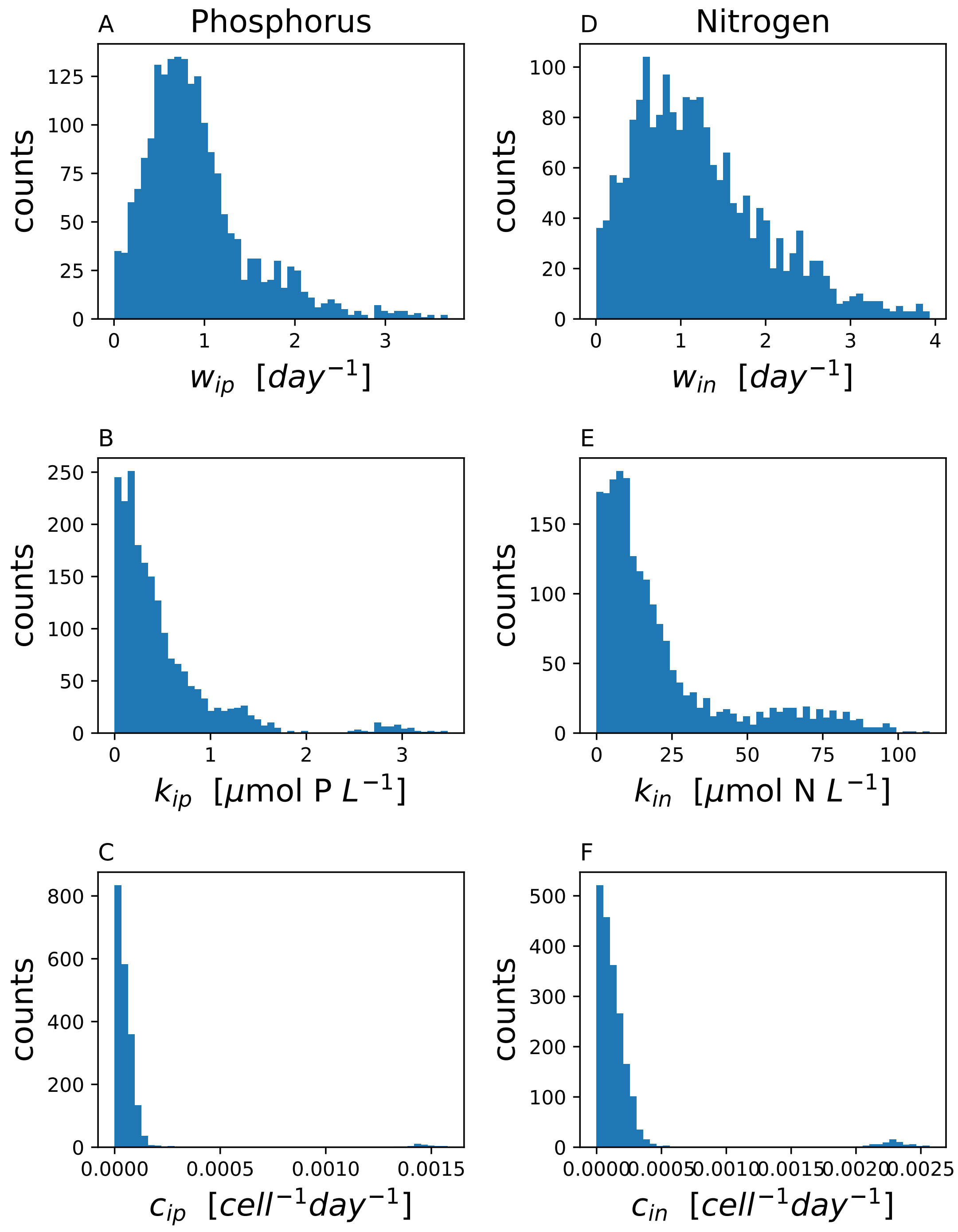

Figure E.1: Distribution of the species traits used in the simulation for species limited by phosphorus and nitrogen.

E.3 Community model fits

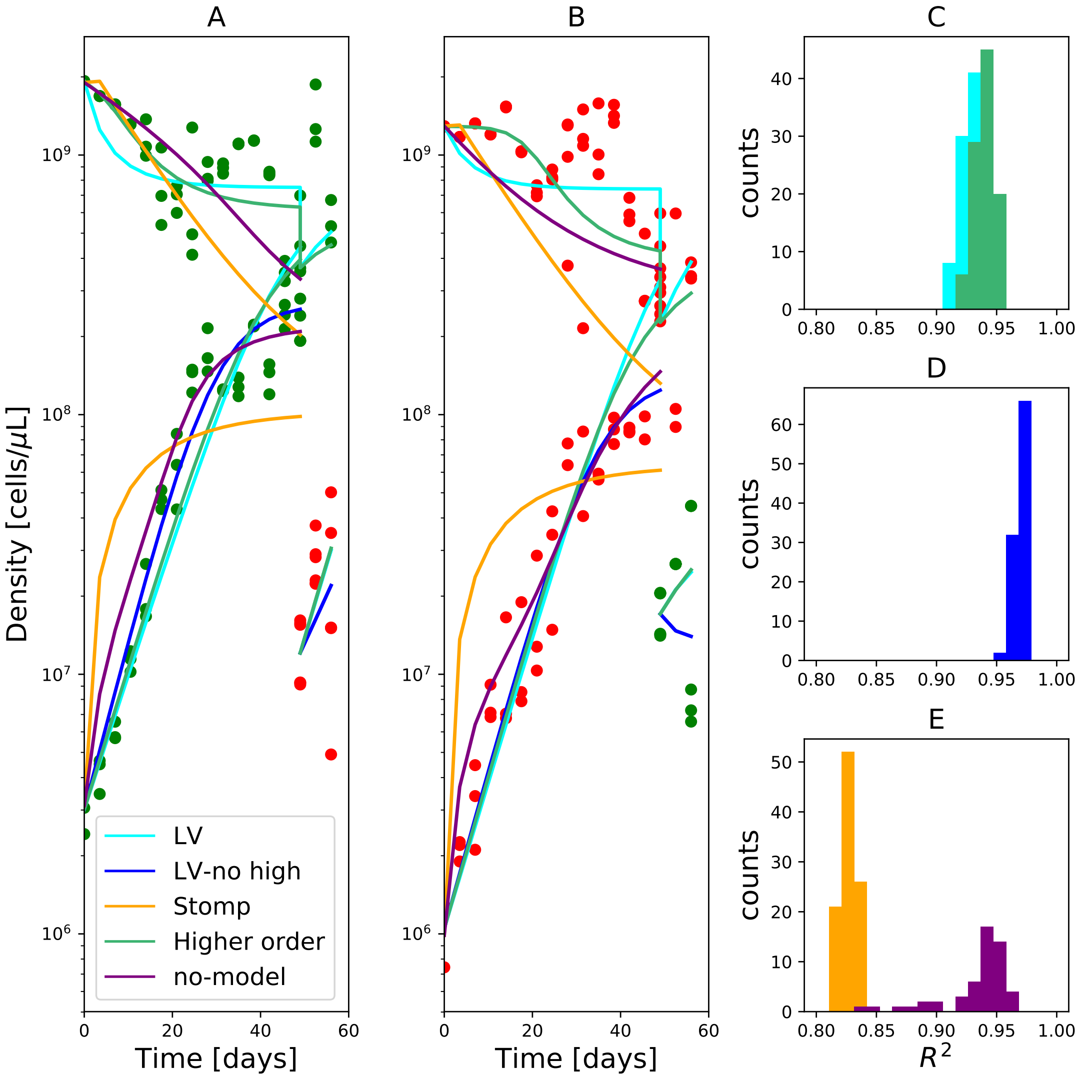

Figure E.2: A,B: Example fits of the different methods to the species density data. C-E: Histograms of the R^2 for all fitted methods to the resampled species density data. All methods fit the data very well. However, we caution that the R^2 between the different methods may not be directly comparable, as they fit different species densities. LV and "Higher order" fit all species densities, "LV no high" fits only monoculture densities from low starting densities and invasion growth rates, and finally Stomp and no-model fit only monoculture densities. Importantly, all community models fit the experimental data quite well (except maybe Stomp), such that R^2 gives only limited possibilities to exclude one community model from the analysis.

Bibliography

Abrams, P. (1980). ARE COMPETITION COEFFICIENTS CONSTANT? INDUCTIVE VERSUS DEDUCTIVE APPROACHES. *The American Naturalist*, 116, 730–735.

Abrams, P. (1983). ARGUMENTS IN FAVOR OF HIGHER ORDER INTERACTIONS. *The American Naturalist*, 121, 887–891.

Adler, P.B., Dalgleish, H.J. & Ellner, S.P. (2012). Forecasting plant community impacts of climate variability and change: When do competitive interactions matter? *Journal of Ecology*, 100, 478–487.

Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: An embarrassment of niches. *Ecology Letters*, 13, 1019–1029.

Adler, P.B., HilleRislambers, J. & Levine, J.M. (2007). A niche for neutrality. *Ecology Letters*, 10, 95–104.

Adler, P.B., Kleinhesselink, A., Hooker, G., Taylor, J.B., Teller, B. & Ellner, S.P. (2018a). Weak interspecific interactions in a sagebrush steppe? Conflicting evidence from observations and experiments. *Ecology*, 99, 1621–1632.

Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M., Tredennick, A.T. & Veblen, K.E. (2018b). Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21, 1319–1329.

Allan, E., Van Ruijven, J. & Crawley, M.J. (2010). Foliar fungal pathogens and grassland biodiversityAllan, E., Van Ruijven, J., & Crawley, M. J. (2010). Foliar fungal pathogens and grassland biodiversity. Ecology, 91(9), 2572–2582. *Ecology*, 91, 2572–2582.

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

Allesina, S. & Tang, S. (2015). The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology*, 57, 63–75.

Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences*, 106, 11641–11645.

Armstrong, R.A. & Mcgehee, R. (1976). Coexistence of species competing for shared resources. *Theoretical Population Biology*, 9, 317–328.

Baert, J.M., Janssen, C.R., Sabbe, K. & De Laender, F. (2016). Per capita interactions and stress tolerance drive stress-induced changes in biodiversity effects on ecosystem functions. *Nature Communications*, 7, 1–8.

Baggio, C.M., J.-P., Di Falco, S., Hertig, A. & Pomati, F. (2018). Economic Behavior, Biodiversity , and Environmental Effects: Evidence from Lake Zurich. *Journal of Environmental Economics and Management*.

Bairey, E., Kelsic, E.D. & Kishony, R. (2016). High-order species interactions shape ecosystem diversity. *Nature Communications*, 7, 1–7.

Balvanera, P., Pfisterer, A.B., N, B., S, H.J., T, N., D, R. & B, S. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9, 1146–1156.

Bannar-Martin, K.H., Kremer, C.T., Ernest, S.K., Leibold, M.A., Auge, H., Chase, J., Declerck, S.A., Eisenhauer, N., Harpole, S., Hillebrand, H., Isbell, F., Koffel, T., Larsen, S., Narwani, A., Petermann, J.S., Roscher, C., Cabral, J.S. & Supp, S.R. (2018). Integrating community assembly and biodiversity to better understand ecosystem function: the Community Assembly and the Functioning of Ecosystems (CAFE) approach. *Ecology Letters*, 21, 167–180.

Barabás, G., D'Andrea, R. & Stump, S.M. (2018). Chesson's coexistence theory. *Ecological Monographs*, 88, 277–303.

Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2016). The effect Of intra- and interspecific competition on coexistence in multispecies communities. *American Naturalist*, 188, E1–E12.

Barabás, G., Pigolotti, S., Gyllenberg, M., Dieckmann, U. & Meszéna, G. (2012). Continuous coexistence or discrete species? A new review of an old question. *Evolutionary Ecology Research*, 14, 523–554.

Bell, G. (2000). The Distribution of Abundance in Neutral Communities. *The American Naturalist*, 155, 606–617.

Benincá, E., Huisman, J., Heerkloss, R., Jöhnk, K.D., Branco, P., Van Nes, E.H., Scheffer, M. & Ellner, S.P. (2008). Chaos in a long-term experiment with a plankton community. *Nature*, 451, 822–825.

Berger, S.A., Diehl, S., Kunz, T.J., Albrecht, D., Oucible, A.M. & Ritzer, S. (2006). Light supply, plankton biomass, and seston stoichiometry in a gradient of lake mixing depths. *Limnology and Oceanography*, 51, 1898–1905.

Best, R.J., Caulk, N.C. & Stachowicz, J.J. (2013). Trait vs. phylogenetic diversity as predictors of competition and community composition in herbivorous marine amphipods. *Ecology Letters*, 16, 72–80.

Bimler, M.D., Stouffer, D.B., Lai, H.R. & Mayfield, M.M. (2018). Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, 106, 1839–1852.

Boyd, P.W. (2002). Environmental factors controlling phytoplankton processes in the Southern Ocean. *Journal of Phycology*, 38, 844–861.

Bricaud, A., Babin, M., Morel, A. & Claustre, H. (1995). Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: Analysis and parametrization. *Journal of Geophysical research*, 100, 13321–13332.

Bricaud, A., Claustre, H., Ras, J. & Oubelkheir, K. (2004). Natural variability of phytoplanktonic absorption in oceanic waters: Influence of the size structure of algal populations. *Journal of Geophysical Research: Oceans*, 109, 1–12.

Cadotte, M.W. (2017). Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters*, 20, 989–996.

Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, 4, 1–9.

Cardinaux, A., Hart, S.P. & Alexander, J.M. (2018). Do soil biota influence the outcome of novel interactions between plant competitors? *Journal of Ecology*, 106, 1853–1863.

Carmel, Y., Cornell, S.J., Belmaker, J., Suprunenko, Y.F., Kent, R., Kunin, W.E. & Bar-Massada, A. (2017). Using exclusion rate to unify niche and neutral perspectives on coexistence. *Oikos*, 126, 1451–1458.

Carpenter, S.R., Armbrust, E.V., Arzberger, P.W., Chapin, F.S., Elser, J.J., Hackett, E.J., Ives, A.R., Kareiva, P.M., Leibold, M.A., Lundberg, P., Mangel, M., Merchant, N., Murdoch, W.W., Palmer, M.A., Peters, D.P.C., Pickett, S.T.A., Smith, K.K., Wall, D.H. & Zimmerman, A.S. (2009). Accelerate Synthesis in Ecology and Environmental Sciences. *BioScience*, 59, 699–701.

Carrara, F., Giometto, A., Seymour, M., Rinaldo, A. & Altermatt, F. (2015). Inferring species interactions in ecological communities: A comparison of methods at different levels of complexity. *Methods in Ecology and Evolution*, 6, 895–906.

Carroll, I.T., Cardinale, B.J. & Nisbet, R.M. (2011). Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology*, 92, 1157–1165.

Carson, W.P. & Root, R.B. (2000). Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs*, 70, 73–99.

Case, T.J. (1981). Niche packing and coevolution in competition communities. *Proceedings of the National Academy of Sciences of the United States of America*, 78, 5021–5025.

Cenci, S. & Saavedra, S. (2018). Structural stability of nonlinear population dynamics. *Physical Review E*, 97.

Chase, J.M. & Leibold, M.A. (2003). Introduction: History, Context, and Purpose. In: *Ecological Niches: Linking Classical and Contemporary Approaches*. March 2017, p. 244.

Chesson, P. (1990). MacArthur's consumer-resource model. *Theoretical Population Biology*, 37, 26–38.

Chesson, P. (1994). Multispecies Competition in Variable Environments. *Theoretical Population Biology*, 45, 227–276.

Chesson, P. (2000). Mechanisms of maintenance of speciesdiversity. *Annual Review of Ecology, Evolution, and Systematics*, 31.

Chesson, P. (2003). Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology*, 64, 345–357.

Chesson, P. (2013). Species Competition and Predation. In: *Ecological Systems*. Springer New York, pp. 223–256.

Chesson, P. & Kuang, J.J. (2008). The interaction between predation and competition. *Nature*, 456, 235–238.

Chesson, P., Pacala, S. & Neuhauser, C. (2001). Environmental niches and ecosystem functioning. *Functional consequences of Biodiversity*, pp. 213–245.

Christensen V. & D., P. (1992). ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, 61, 169–185.

Chu, C. & Adler, P.B. (2015). Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecological Monographs*, 85, 373–392.

Clark, A.D., Deffner, D., Laland, K., Odling-Smee, J. & Endler, J. (2019a). Niche construction affects the variability and strength of natural selection. *The American Naturalist*, 195.

Clark, A.T., Hillebrand, H. & Harpole, W.S. (2019b). Scale both confounds and informs characterization of multi-species coexistence in empirical systems. *The American Naturalist*, p. 705826.

Connolly, S.R., Hughes, T.P. & Bellwood, D.R. (2017). A unified model explains commonness and rarity on coral reefs. *Ecology Letters*, 20, 477–486.

De Laender, F., Rohr, J.R., Ashauer, R., Baird, D.J., Berger, U., Eisenhauer, N., Grimm, V., Hommen, U., Maltby, L., Meliàn, C.J., Pomati, F., Roessink, I., Radchuk, V. & Van den Brink, P.J. (2016). Reintroducing Environmental Change Drivers in Biodiversity–Ecosystem Functioning Research. *Trends in Ecology and Evolution*, 31, 905–915.

Degen, R., Aune, M., Bluhm, B.A., Cassidy, C., Monika, K., Kraan, C., Vandepitte, L., Maria, W., Zhulay, I., Albano, P.G., Bremner, J., Grebmeier, J.M., Link, H., Morata, N., Nordström, M.C., Ghodrati, M., Sutton, L. & Zuschin, M. (2018). Trait-based approaches in rapidly changing ecosystems : A roadmap to the future polar oceans. *Ecological Indicators*, 91, 722–736.

Edwards, K.F., Kremer, C.T., Miller, E.T., Osmond, M.M., Litchman, E. & Klausmeier, C.A. (2018). Evolutionarily stable communities: a framework for understanding the role of trait evolution in the maintenance of diversity. *Ecology Letters*, 21, 1853–1868.

Edwards, K.F. & Stachowicz, J.J. (2012). Temporally varying larval settlement , competition , and coexistence in a sessile invertebrate community. *Marine Ecology Progress Series*, 462, 93–102.

Edwards, K.F., Thomas, M.K., Klausmeier, C.A. & Litchman, E. (2015). Light and growth in marine phytoplankton: Allometric, taxonomic, and environmental variation. *Limnology and Oceanography*, 60, 540–552.

Ellner, S.P., Snyder, R.E. & Adler, P.B. (2016). How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters*, 19, 1333–1342.

Ellner, S.P., Snyder, R.E., Adler, P.B. & Hooker, G. (2019). An expanded modern coexistence theory for empirical applications. *Ecology Letters*.

Emmerson, M.C. & Raffaelli, D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73, 399–409.

Estrada, M., Henriksen, P., Gasol, J.M., Casamayor, E.O. & Pedrós-Alió, C. (2004). Diversity of planktonic photoautotrophic microorganisms along a salinity gradient as depicted by microscopy, flow cytometry, pigment analysis and DNA-based methods. *FEMS Microbiology Ecology*, 49, 281–293.

Etienne, R.S., Cabral, J.S., Hagen, O., Hartig, F., Hurlbert, A.H., Pellissier, L., Pontarp, M. & Storch, D. (2019). A minimal model for the latitudinal diversity gradient suggests a dominant role for ecological limits. *American Naturalist*, 194, E122–E133.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., Field, C.B., Behrenfeld, M.J. & Randerson, J.T. (2009). Primary Production of the Biosphere : Integrating Terrestrial and Oceanic Components. *Science*, 281, 237–240.

Fietz, S. & Nicklisch, A. (2004). An HPLC analysis of the summer phytoplankton assemblage in Lake Baikal. *Freshwater Biology*, 49, 332–345.

Fontaine, C., Guimarães, P.R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H., van Veen, F.J. & Thébault, E. (2011). The ecological and evolutionary implications of merging different types of networks. *Ecology Letters*, 14, 1170–1181.

Fort, H. (2018). On predicting species yields in multispecies communities: Quantifying the accuracy of the linear Lotka-Volterra generalized model. *Ecological Modelling*, 387, 154–162.

Fox, J.W. (2005). Interpreting the 'selection effect' of biodiversity on ecosystem function. *Ecology Letters*, 8, 846–856.

Fukami, T., Mordecai, E.A. & Ostling, A. (2016). A framework for priority effects. *Journal of Vegetation Science*, 27, 655–657.

Gallego, I., Venail, P. & Ibelings, B.W. (2019). Size differences predict niche and relative fitness differences between phytoplankton species but not their coexistence. *ISME Journal*.

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

Gause, G.F. (1934). *The struggle for existence*. Williams and Wilkins, Baltimore.

Gerla, D.J., Mooij, W.M. & Huisman, J. (2011). Photoinhibition and the assembly of light-limited phytoplankton communities. *Oikos*, 120, 359–368.

Germain, R., Weir, J. & Gilbert, B. (2016). Species coexistence: macroevolutionary patterns and the contigency of historical interactions. *PRSB*, 283, 20160047.

Godoy, O., Bartomeus, I., Rohr, R.P. & Saavedra, S. (2018). Towards the Integration of Niche and Network Theories.

Godoy, O., Gómez-aparicio, L., Pérez-ramos, I.M. & Allan, E. (2020). An excess of niche differences maximizes ecosystem functioning. *Nature Communications*, pp. 1–10.

Godoy, O., Kraft, N.J. & Levine, J.M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17, 836–844.

Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.

Godoy, O., Stouffer, D.B., Kraft, N.J. & Levine, J.M. (2017). Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology*, 98, 1193–1200.

Godwin, C.M., Chang, F.H. & Cardinale, B.J. (2020). An empiricist's guide to modern coexistence theory for competitive communities. *Oikos*.

Goh, B. & Jennings, L. (1977). No Feasibility and stability in randomly assembled Lotka-Volterra models. *Ecological Modelling*, 3.

Goldman, J., McCarthy, J. & Peavey, D. (1979). Growth rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature*, 279.

Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hautier, Y., Hillebrand, H., Lind, E.M., Pärtel, M., Bakker, J.D., Buckley, Y.M., Crawley, M.J., Damschen, E.I., Davies, K.F., Fay, P.A., Firn, J., Gruner, D.S., Hector, A., Knops, J.M., MacDougall, A.S., Melbourne, B.A., Morgan, J.W., Orrock, J.L., Prober, S.M., Smith, M.D. & Rinke_suppl (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393.

Grainger, T.N., Letten, A.D., Gilbert, B. & Fukami, T. (2019a). Applying modern coexistence theory to priority effects. *Proceedings of the National Academy of Sciences*, 116, 6205–6210.

Grainger, T.N., Levine, J.M. & Gilbert, B. (2019b). The Invasion Criterion: A Common Currency for Ecological Research. *Trends in Ecology and Evolution*, 34, 925–935.

Grilli, J., Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2017). Higher-order interactions stabilize dynamics in competitive network models. *Nature*, 548, 210–213.

Gross, N., Bagousse-Pinguet, Y.L., Liancourt, P., Berdugo, M., Gotelli, N.J. & Maestre, F.T. (2017). multifunctionality. *Nature Ecology and Evolution*, 1, 1–9.

Hardin, G. (1960). The competitive exclusion principle.

Harpole, W.S. & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, 446, 791–793.

Harris, K., Parsons, T.L., Ijaz, U.Z., Lahti, L., Holmes, I. & Quince, C. (2017). Linking Statistical and Ecological Theory: Hubbell's Unified Neutral Theory of Biodiversity as a Hierarchical Dirichlet Process: This paper addresses the issue of a species occupying a specific ecological niche by introducing a new algorithmic model that . In: *Proceedings of the IEEE*.

Hart, S.P., Freckleton, R.P. & Levine, J.M. (2018). How to quantify competitive ability. *Journal of Ecology*, 106, 1902–1909.

Hart, S.P., Schreiber, S.J. & Levine, J.M. (2016). How variation between individuals affects species coexistence. *Ecology Letters*, 19, 825–838.

Hart, S.P., Turcotte, M.M. & Levine, J.M. (2019). Effects of rapid evolution on species coexistence. *Proceedings of the National Academy of Sciences*, 116, 2112–2117.

Hausch, S., Vamosi, S.M. & Fox, J.W. (2018). Effects of intraspecific phenotypic variation on species coexistence. *Ecology*, 99, 1453–1462.

Hector, A. & Loreau, M. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.

HilleRisLambers, J., Adler, P., Harpole, W., Levine, J. & Mayfield, M. (2012). Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248.

Holt, R., Grover, J. & Tilman, D. (1994). Simple Rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*, 144, 741–771.

Holt, R.D. (1977). Predation, Apparend Competition, and the Structure of Prey Communities. *Theoretical Population Biology*, 229, 197–229.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, New Jersey.

Huisman, J. & Weissing, F.J. (1994). Light-Limited Growth and Competition for Light in Well-Mixed Aquatic Environments : An Elementary Model. *Ecology*, 75, 507–520.

Huisman, J. & Weissing, F.J. (1999). Biodiversity of plankton by species oscillations and chaos. *Nature*, 402, 407–410.

Hurlbert, S.H. (1978). The Measurement of Niche Overlap and Some Relatives.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.

Hutchinson, G.E. (1959). HOMAGE TO SANTA ROSALIA or WHY ARE THERE SO MANY KINDS OF ANIMALS?* G. *The american Natrualist*, XCIII.

Irigoien, X., Huisman, J. & Harris, R.P. (2004). Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature*, 429, 863–867.

Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P. & Gravel, D. (2016). No complexity-stability relationship in empirical ecosystems. *Nature Communications*, 7, 1–8.

Johnson, C.A. & Bronstein, J.L. (2019). Coexistence and competitive exclusion in mutualism. *Ecology*, 100.

Ke, P.J. & Letten, A.D. (2018). Coexistence theory and the frequency-dependence of priority effects. *Nature Ecology and Evolution*, 2, 1691–1695.

Keddy, P.A. & Shipley, B. (1989). Competitive heirarchies in herb plant communities.

Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. *PLoS Biology*, 14, 1–21.

KEYMER, I.F. (1983). Diseases of squirrels in Britain. *Mammal Review*, 13, 155–158.

Kingsland, S. (2015). Alfred J. Lotka and the origins of theoretical population ecology. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 9493–9495.

Kingsland, S.E. (1995). *Modeling Nature: Episodes in the History of Population Ecology*. University of CHicago Press.

Kokkoris, G.D., Jansen, V.A.A., Loreau, M. & Troumbis, A.Y. (2002). Variability in interaction strength and implications for biodiversity. *Journal of Animal Ecology*, 71, 362–371.

Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, 112, 797–802.

Kremer, C.T. & Klausmeier, C.A. (2017). Species packing in eco-evolutionary models of seasonally fluctuating environments. *Ecology Letters*, 20, 1158–1168.

Kulkarni, D. & De Laender, F. (2017). The combined effects of biotic and abiotic stress on species richness and connectance. *PLoS ONE*, 12, 1–15.

Langdon, C. (1988). On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. II. A general review. *Journal of Plankton Research*, 10, 1291–1312.

Lanuza, J.B., Bartomeus, I. & Godoy, O. (2018). Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. *Ecology Letters*, 21, 865–874.

Lavallée, B.F. & Pick, F.R. (2002). Picocyanobacteria abundance in relation to growth and loss rates in oligotrophic to mesotrophic lakes. *Aquatic Microbial Ecology*, 27, 37–46.

Lawton, J.A. (1999). Are there general laws in ecology? *Oikos*, 84, 177–192.

Letten, A.D., Dhami, M.K., Ke, P.J. & Fukami, T. (2018). Species coexistence through simultaneous fluctuation-dependent mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 6745–6750.

Letten, A.D., Ke, P.J. & Fukami, T. (2017). Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs*, 87, 161–177.

Letten, A.D. & Stouffer, D.B. (2019). The mechanistic basis for higher-order interactions and non-additivity in competitive communities. *Ecology Letters*, 22, 423–436.

Levin, S. (1970). Community equilibria and stability, and an extension of the competitive exclusion principle. *The american naturalist*, 104, 185–193.

Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56–64.

Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.

Litchman, E. & Klausmeier, C.A. (2001). Competition of Phytoplankton under Fluctuating Light. *The American Naturalist*, 157, 170–187.

Litchman, E. & Klausmeier, C.A. (2008). Trait-Based Community Ecology of Phytoplankton. *Annual Review of Ecology, Evolution, and Systematics*, 39, 615–639.

Loreau, M. (2004). Does functional redundancy exist? *Oikos*, 104, 606–611.

Lotka, A.J. (1920). ANALYTICAL NOTE ON CERTAIN RHYTHMIC RELATIONS [N ORGANIC SYSTEMS. *PNAS*, pp. 410–415.

MacArthur, R. (1970). Species packing and competitive equilibrium for many species. *Theoretical Population Biology*, 1, 1–11.

MacArthur, R. & Levins, R. (1964). Competition, Habitat Selection, and Character Displacement in a Patchy Environment. *Proceedings of the National Academy of Sciences of the United States of America*, 51, 1207–1210.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gabriel Gatica, M., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D. & Zaady, E. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, 335, 214–218.

Matías, L., Godoy, O., Gómez-Aparicio, L. & Pérez-Ramos, I.M. (2018). An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks. *Journal of Ecology*, 106, 826–837.

May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.

Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093.

Mayfield, M.M. & Stouffer, D.B. (2017). Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecology and Evolution*, 1, 1–7.

Maynard, D.S., Wootton, J.T., Serván, C.A. & Allesina, S. (2019). Reconciling empirical interactions and species coexistence. *Ecology Letters*, 22, 1028–1037.

Mcgill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21.

McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kieland, K., Kwiatkowski, B.L., Laundre, J.A. & Murray, G. (2002). Resource-based niche provide a basis for plant species\rdiversity and dominance in arctic tundra. *Nature*, 415, 68–71.

Meszéna, G., Gyllenberg, M., Pásztor, L. & Metz, J.A. (2006). Competitive exclusion and limiting similarity: A unified theory. *Theoretical Population Biology*, 69, 68–87.

Mickalide, H. & Kuehn, S. (2019). Higher-order interaction inhibits bacterial invasion of a phototroph-predator microbial community. *bioRxiv*, p. 564260.

Moll, J. & Brown, J. (2008). Competition and Coexistence with Multiple Life-History Stages. *The American Naturalist*, 171, 839–843.

Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264.

Moore, J.C., De Ruiter, P.C., Hunt, H.W., Coleman, D.C. & Freckman, D.W. (1996). Microcosms and soil ecology: Critical linkages between field studies and modelling food webs. *Ecology*, 77, 694–705.

Mordecai, E.A. (2011). Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. *Ecological Monographs*, 81, 429–441.

Morisita, M. (1959). Measuring of Interspecific Association and Similarity Between Communities.

Napier, J.D., Mordecai, E.A. & Heckman, R.W. (2016). The role of drought- and disturbance-mediated competition in shaping community responses to varied environments. *Oecologia*, 181, 621–632.

Narwani, A., Alexandrou, M.A., Oakley, T.H., Carroll, I.T. & Cardinale, B.J. (2013). Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, 16, 1373–1381.

Narwani, A., Bentlage, B., Alexandrou, M.A., Fritschie, K.J., Delwiche, C., Oakley, T.H. & Cardinale, B.J. (2017). Ecological interactions and coexistence are predicted by gene expression similarity in freshwater green algae. *Journal of Ecology*, 105, 580–591.

Olsen, S.L., Töpper, J.P., Skarpaas, O., Vandvik, V. & Klanderud, K. (2016). From facilitation to competition: Temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology*, 22, 1915–1926.

Pande, J., Fung, T., Chisholm, R. & Shnerb, N.M. (2019). Mean growth rate when rare is not a reliable metric for persistence of species. *Ecology Letters*.

Passarge, J., Hol, S., Escher, M. & Huisman, J. (2006). Competition for nutrients and light: Stable coexistence, alternative stable states, or competitive exclusion? *Ecological Monographs*, 76, 57–72.

Patel, S. & Schreiber, S.J. (2018). Robust permanence for ecological equations with internal and external feedbacks. *Journal of Mathematical Biology*, 77, 79–105.

Pérez-Ramos, I.M., Matías, L., Gómez-Aparicio, L. & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, 10, 1–11.

Petry, W.K., Kandlikar, G.S., Kraft, N.J., Godoy, O. & Levine, J.M. (2018). A competition–defence trade-off both promotes and weakens coexistence in an annual plant community. *Journal of Ecology*, 106, 1806–1818.

Pillai, P., Gonzalez, A. & Loreau, M. (2011). Metacommunity theory explains the emergence of food web complexity. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 19293–19298.

Poisot, T., LaBrie, R., Larson, E., Rahlin, A. & Simmons, B.I. (2019). Data-based, synthesis-driven: Setting the agenda for computational ecology. *Ideas in Ecology and Evolution*, 12, 9–21.

Primeau, F.W., Holzer, M. & DeVries, T. (2013). Southern Ocean nutrient trapping and the efficiency of the biological pump. *Journal of Geophysical Research: Oceans*, 118, 2547–2564.

Radchuk, V., Laender, F.D., Cabral, J.S., Boulangeat, I., Crawford, M., Bohn, F., Raedt, J.D., Scherer, C., Svenning, J.C., Thonicke, K., Schurr, F.M., Grimm, V. & Kramer-Schadt, S. (2019). The dimensionality of stability depends on disturbance type. *Ecology Letters*, 22, 674–684.

Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F. & Eisenhauer, N. (2012). Impacts of biodiversity loss escalate through time as redundancy fades. *Science*, 336, 589–592.

Renkonen, O. (1938). Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Societas zoologica-botanica Fennica Vanamo*.

Rey, P.J., Manzaneda, A.J. & Alc, J.M. (2017). The interplay between aridity and competition determines colonization ability , exclusion and ecological segregation in the heteroploid Brachypodium distachyon species complex. pp. 85–96.

Rip, J.M. & Mccann, K.S. (2011). Cross-ecosystem differences in stability and the principle of energy flux. *Ecology Letters*, 14, 733–740.

Roughgarden, J. (1976). Resource partitioning among competing species—A coevolutionary approach. *Theoretical Population Biology1*, 9, 388–424.

Roughgarden, J. (1979). *Theory of Population Genetics and Ecolutionary Ecology*. Macmillan, New York.

Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J. & Levine, J.M. (2017). A structural approach for understanding multispecies coexistence. *Ecological Monographs*, 87, 470–486.

Sakavara, A., Tsirtsis, G., Roelke, D.L., Mancy, R. & Spatharis, S. (2017). Lumpy species coexistence arises robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences*, p. 201705944.

Schreiber, S.J. (2000). Criteria for Cr robust permanence. *Journal of Differential Equations*, 162, 400–426.

Schreiber, S.J. (2017). *Coexistence in the Face of Uncertainty*. vol. 79.

Schreiber, S.J., Yamamichi, M. & Strauss, S.Y. (2019). When rarity has costs: coexistence under positive frequency-dependence and environmental stochasticity. *Ecology*, 100, e02664.

Sen, P.K. (1968). Estimates of the Regression Coefficient Based on Kendall's Tau. *Journal of the American Statistical Association*, 63, 1379–1389.

Serván, C.A., Capitán, J.A., Grilli, J., Morrison, K.E. & Allesina, S. (2018). Coexistence of many species in random ecosystems. *Nature Ecology and Evolution*, 2, 1237–1242.

Siefert, A., Zillig, K.W., Friesen, M.L. & Strauss, S.Y. (2018). Mutualists Stabilize the Coexistence of Congeneric Legumes. *The American Naturalist*, 193, 200–212.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology and Evolution*, 19, 605–611.

Six, C., Thomas, J.C., Garczarek, L., Ostrowski, M., Dufresne, A., Blot, N., Scanlan, D.J. & Partensky, F. (2007). Diversity and evolution of phycobilisomes in marine Synechococcus spp.: A comparative genomics study. *Genome Biology*, 8.

Song, C., Barabás, G. & Saavedra, S. (2019). On the consequences of the interdependence of stabilizing and equalizing mechanisms. *The American Naturalist*, pp. 000–000.

Song, C., Rohr, R.P. & Saavedra, S. (2018). A guideline to study the feasibility domain of multi-trophic and changing ecological communities. *Journal of Theoretical Biology*, 450, 30–36.

Song, C., Rohr, R.P., Vasseur, D. & Saavedra, S. (2020a). Disentangling the effects of external perturbations on coexistence and priority effects. *Journal of Ecology*, 108, 1677–1689.

Song, C. & Saavedra, S. (2020). Telling ecological networks apart by their structure: An environment-dependent approach. *PLOS Computational Biology*, 16, e1007787.

Song, C., Von Ahn, S., Rohr, R.P. & Saavedra, S. (2020b). Towards a Probabilistic Understanding About the Context-Dependency of Species Interactions.

Spaak, J.W., Baert, J.M., Baird, D.J., Eisenhauer, N., Maltby, L., Pomati, F., Radchuk, V., Rohr, J.R., Van den Brink, P.J. & De Laender, F. (2017). Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. *Ecology Letters*, 20, 1315–1324.

Spaak, J.W., Carpentier, C. & Laender, F.D. (2019). Fitness differences, not niche differences, limit species richness. *bioRxiv*.

Spaak, J.W. & De Laender, F. (2020). Intuitive and broadly applicable definitions of niche and fitness differences. *Ecology Letters*, p. doi: https://doi.org/10.1101/482703.

Srivastava, D.S. & Vellend, M. (2005). Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation? *Annual Review of Ecology, Evolution, and Systematics*, 36, 267–294.

Stomp, M., Huisman, J., De Jongh, F., Veraart, A.J., Gerla, D., Rijkeboer, M., Ibelings, B.W., Wollenzien, U.I. & Stal, L.J. (2004). Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature*, 432, 104–107.

Stomp, M., Huisman, J., Stal, L.J. & Matthijs, H.C. (2007a). Colorful niches of phototrophic microorganisms shaped by vibrations of the water molecule. *ISME Journal*, 1, 271–282.

Stomp, M., Huisman, J., Vörös, L., Pick, F.R., Laamanen, M., Haverkamp, T. & Stal, L.J. (2007b). Colourful coexistence of red and green picocyanobacteria in lakes and seas. *Ecology Letters*, 10, 290–298.

Striebel, M., Behl, S., Diehl, S. & Stibor, H. (2009). Spectral Niche Complementarity and Carbon Dynamics in Pelagic Ecosystems. *The American Naturalist*, 174, 141–147.

Striebel, M., Singer, G., Stibor, H. & Andersen, T. (2012). "Trophic overyielding": Phytoplankton diversity promotes zooplankton productivity. *Ecology*, 93, 2719–2727.

Taper, M. & Case, T.J. (1985). Quantitative Genetic models for the coevolution of character displacement. *Ecology*, 66, 355–371.

Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853–856.

Tilman, D. (1996). Biodiversity: Population versus Ecosystem Stability.

Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471–493.

Tilman, G.D. (1982). *Resource Competition and Community Structure*. Princeton university press.

Traill, L.W., Lim, M.L., Sodhi, N.S. & Bradshaw, C.J. (2010). Mechanisms driving change: Altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology*, 79, 937–947.

Tredennick, A.T., Adler, P.B. & Adler, F.R. (2017). The relationship between species richness and ecosystem variability is shaped by the mechanism of coexistence. *Ecology Letters*, 20, 958–968.

Turelli, M. (1978). Does environmental variability limit niche overlap? *Proceedings of the National Academy of Sciences of the United States of America*, 75, 5085–9.

Turnbull, L.A., Levine, J.M., Loreau, M. & Hector, A. (2013). Coexistence, niches and biodiversity effects on ecosystem functioning. *Ecology Letters*, 16, 116–127.

Usinowicz, J., Chang-Yang, C.H., Chen, Y.Y., Clark, J.S., Fletcher, C., Garwood, N.C., Hao, Z., Johnstone, J., Lin, Y., Metz, M.R., Masaki, T., Nakashizuka, T., Sun, I.F., Valencia, R., Wang, Y., Zimmerman, J.K., Ives, A.R. & Wright, S.J. (2017). Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity. *Nature*, 550, 105–108.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M. & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, 29, 299–307.

Van Den Hoek, C., Mann, D.G. & Jahns, H.M. (1995). Algae: an introduction to phycology.

Vellend, M. (2016). *The theory of ecological communities*. Princeton University Press.

Venail, P.A., Narwani, A., Fritschie, K., Alexandrou, M.A., Oakley, T.H. & Cardinale, B.J. (2014). The influence of phylogenetic relatedness on species interactions among freshwater green algae in a mesocosm experiment. *Journal of Ecology*, 102, 1288–1299.

Veresoglou, S.D., Rillig, M.C. & Johnson, D. (2018). Responsiveness of plants to mycorrhiza regulates coexistence. *Journal of Ecology*, 106, 1864–1875.

Violle, C., Nemergut, D.R., Pu, Z. & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, 14, 782–787.

Volterra, V. (1926). Variazioni flultuazioni del numero d'invididui in specie convirenti. *Men Acad Lincei*, 2, 31–113.

Wainwright, C.E., HilleRisLambers, J., Lai, H.R., Loy, X. & Mayfield, M.M. (2019). Distinct responses of niche and fitness differences to water availability underlie variable coexistence outcomes in semi-arid annual plant communities. *Journal of Ecology*, 107, 293–306.

Walsh, M.R. (2013). The evolutionary consequences of indirect effects. *Trends in Ecology & Evolution*, 28, 23–29.

Zarnetske, P.L., Gouhier, T.C., Hacker, S.D., Seabloom, E.W. & Bokil, V.A. (2013). Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *Journal of Ecology*, 101, 905–915.

Zepeda, V. & Martorell, C. (2019). Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. *Ecology*, 0, e02726.

Zhao, L., Zhang, Q.G. & Zhang, D.Y. (2016). Evolution alters ecological mechanisms of coexistence in experimental microcosms. *Functional Ecology*, 30, 1440–1446.

Zhao, Q., Van den Brink, P.J., Carpentier, C., Wang, Y.X.G., Rodríguez-Sánchez, P., Xu, C., Vollbrecht, S., Gillissen, F., Vollebregt, M., Wang, S. & De Laender, F. (2019). Horizontal and vertical diversity jointly shape food web stability against small and large perturbations. *Ecology Letters*, pp. 1152–1162.