**Mapping species niche and fitness differences**

**for communities with multiple interaction types**

**Abstract**

Modern coexistence theory (MCT) holds the potential to study the ability of species to avoid extinction (i.e. to persist) across community types but is rarely applied beyond pairs of competing species. Here, we show that this limitation can be overcome by mapping species according to their niche () and fitness differences (). This application provides three main benefits to study processes of multispecies persistence across trophic levels. First, - 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* (facilitation and mutualism), and whether persistenceis *possible without the presence of other species* because of trophic interactions such as herbivory or predation. Therefore, this mapping can be seen as a toolbox to describe how species persistence depends on species interactions. Second, - mapping facilitates studying how species persistence responds to environmental changes that shift intrinsic growth rates and the strength and sign of species interactions. Third, - mapping has the potential to foster synthesis across community types because it can accommodate co-occurrence of positive, negative, and neutral interactions between species. We therefore argue that - mapping can promote collaboration across sub-fields, as it provides a common concept to link disparate ecological communities.

**Keywords:** coexistence theory, community assembly, frequency dependence, positive interactions, trophic position.

**From listing species interactions to mapping species**

Ecological communities contain a variety of interaction types, including positive, negative and neutral interactions such as competition, predation, facilitation or mutualism, or amensalism [1]. 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 [2]. Understanding how species can persist amongst this amalgam of trophic and non-trophic interactions is generally considered intractable so different communities containing different interaction types are typically treated independently ([3] but see [4]–[6]). While specialization improves understanding of the details of specific community types, it does not necessarily lead to a broader, system-independent understanding.

Modern coexistence theory (MCT) holds the potential to identify similarities and differences among community types in how species persist, i.e. avoid local extinction in the long-term [7]–[9]. MCT has been used to study a variety of problems dealing with, for instance, eco-evolutionary dynamics [10], [11], global change effects, and macroecological dynamics [12]. The main objective of MCT is to study species *coexistence* (see Glossary) or more generally the *persistence* of single species. Two key concepts in MCT are *niche differences* and *fitness differences* (see a brief historical overview of these two concepts in Box 1). Niche differences measure to what extent the strength of intraspecific interactions exceed the strength of interspecific interactions [7]. High niche differences promote persistence, as they stabilize the dynamics of competing species by buffering a rare species from interspecific competition. Conversely, fitness differences measure differences in competitive ability between species [8]. The strength of a species´ competitive ability is the combination of their ability to grow in the absence of interactions and their sensitivity to competition. A highly competitive species will have a high intrinsic growth rate, low sensitivity to competition, or a combination of both [13], [14]. High values of fitness differences hamper persistence and in the absence of niche differences determine the competitive superior species. Traditionally, niche and fitness differences have been studied for only a small subset of community types containing few species competing for shared resources (e.g. annual plants, plankton, yeast, bacteria) [12], [15], [16]. Alternative interactions such as facilitation or mutualism typically are not considered (but see [17], [18]), either because available methods cannot compute niche and fitness differences in the presence of positive interactions [19] or lack the ability to predict persistence of interacting species pairs when they can [20].

Recent definitions of niche and fitness differences overcome these limitations (Box 2). These theoretical advances allow studying the determinants of species persistence in ways that transcend the specific type of interactions occurring in a given ecological community. Therefore, it is possible to understand in a universal way why species persist, regardless of their particular guild, trophic position, or the sign and size of its interactions with other community members. The first step towards such understanding is to compute niche and fitness differences, which we will denote as and hereafter, where the subscript indicates that they are species-specific quantities in our framework (see box 2 and [20]). More specifically, and can be understood as axes that allow locating the species coordinates across a coexistence map, much like latitude and longitude provides information on spatial location on a regular map. We identify the following three reasons why this - map provides novel avenues of research that can be of general interest to a broad range of researchers. First, the - map generalizes previous work including stabilizing and equalizing mechanisms [7], [21] or priority effects [22] among many other concepts determining population dynamics of interacting species for common resources such as food or space as well as natural enemies [23] (Figure 1). Second, the - map helps to visualize the overall effect of changes of the community dynamics, for example as a result of environmental change. Third, the - map is broadly applicable, which allows comparisons between various different empirical or modelled communities. Therefore, we envision the - map as a general currency to compare different research fields.

**Mapping and to categorize species and community types**

The utility of mapping and lies in its connection to three high-level processes that determine species coexistence, namely *frequency dependence*, the occurrence of *positive species interactions* and whether *persistence is possibl*e without the presence of other species (see Box 2 and Figure 2). One of the most well-studied processes of species persistence in a given community is *frequency dependence*, the first high-level process. Positive frequency dependence (, see Appendix 4 and [22] for a mathematical derivation of this criterion) occurs when intraspecific interactions are weaker than interspecific interactions, i.e. species limit themselves less than other species. Conversely, negative frequency dependence () occurs when intraspecific interactions are stronger than interspecific interactions and both are negative, i.e. species limit themselves more than other species. The second high-level process is the *occurrence of positive species interactions* (, see Appendix 4 and [20]), which are widespread in nature, but of which it is unclear how they contribute to maintain diversity [17]. Finally, the last high-level process is whether *persistence* is *possible* without niche differences, i.e. (, see Appendix 4), not possible without niche differences () or whether *persistence* is *only possible* in the presence of other species (). These high-level processes might occur simultaneously in multispecies communities and are species-specific. The - map can visually represent the high-level processes for each individual species in a multispecies community (Figure 2).

These high-level processes can help advance several seemingly disconnected research fields. For example, frequency dependence and positive species interactions are conceptually connected, as they represent in essence < 1 and > 1, respectively. Yet, these have been treated completely independent from each other in the literature (see e.g. [22], [24] for frequency dependence and [17], [25] for positive species interactions). Also, the identification of these three processes can help formalise terminology that has proven challenging to pinpoint such as priority effects [26], [27]. Priority effects, the idea that species arrival order may affect species composition, have sometimes been linked to communities with alternative stable states or communities that lack a stable attractor [22], [27]. When the specific arrival order of species is random, these communities may appear to be driven by stochastic processes [22]. However, while represent communities purely driven by stochastic forces (i.e. neutrality), the case of priority effects (Figure 4A “priority effects”, sensu [12], [28]) occurs when species can grow when alone (), but cannot invade the community () because they experience positive frequency dependence ().

Different combinations of these high-level processes can help distinguish two different mechanisms by which positive interactions contribute to species persistence. The map formalizes the idea that a facultative mutualist species, e.g. certain microbes or plants, can profit from positive interactions with other species (, Figure 4A facultative mutualists). However, its persistence does not hinge on the presence of other species ( ), i.e. species realise positive growth when grown alone and do not *need* the presence of other community members. Meanwhile, an obligate mutualist such as a pollinator species persists because of positive interactions and this persistence is only possible because of the presence of other species (). Importantly, another pairwise combination of high-level processes, the one corresponding to negative frequency dependence (first high-level process) and positive interactions (second high-level process), is expected to be common in ecological communities that contain asymmetric species interactions such as “competition-facilitation” or prey-predator communities (Figure 4A “competition-facilitation”). Because these communities are among the most- and best-studied by ecologists, the - map can be seen as a new tool to revisit this information and quantitatively assess the relative importance of negative and positive interactions for species persistence within ecological communities [29].

These different combinations of high-level processes may arise through any underlying mechanistic model. For example, priority effects might arise through a large set of mechanisms such as resource and space competition [9], [30], apparent competition [31], [32], chemical warfare, competition for mutualists [25] or any combination of these [33]. Similarly, a community driven by resource competition may give rise to both negative or positive frequency dependence. Therefore, the - map does not map underlying mechanistic interactions, but rather it tracks the resulting high-level processes (see Appendix 1). This may reveal new insights, for example a community driven by predation might be governed by the same high-level processes as a community with obligate mutualists.

The - map offers two complementary perspectives on persistence that differ in their focus. On the one hand, we can adopt a species-level perspective, as the - map provides information on which processes determine the persistence or exclusion of each specific species. Knowing the identity of the species that is predicted to be extinct or that acts as a superior competitor is relevant for many fields in ecology such as conservation biology and biological invasions. and are defined at the species-level with respect to the rest of the community members and therefore incorporate the responses of every species to ecological interactions. Figure 4B provides an example of the information contained in the - map at both the community and the species level. In this mutualistic network with five species, the simultaneous categorization of the three high level processes reveals that (1) plants (dot, cross, diamond) do not need positive interactions while the pollinators (plus and star) do; (2) pollinators acquire a net benefit () from species interactions; (3) one plant species benefits from species interactions and two plant species experience a net negative effect of species interactions. Point (1) and (2) can be gauged directly from the intrinsic growth rates and the interaction matrix, but the - map offers an additional quantitative measure of *how much* the species benefit from species interactions. Additionally, point (3) cannot be obtained easily from the interaction matrix, as all plants have both positive and negative species interactions, but only one plant benefits overall from species interactions.

On the other hand, we can focus on the community-level perspective, in which multiple species are entangled in a complex network. Species in the most simple multispecies community involving three species can interact directly and linearly, directly via higher order interactions (HOIs) which occur when a third species modifies the per capita effects between two interacting species [34], or indirectly by affecting the density of other species. Previous work has shown how all these types of interactions contribute to species‘ fitness [35], but their implications for species coexistence within ecological communities remains unclear. This gap can be filled by connecting the - map to ecological theory studying the stability of ecological communities, because the definitions of and are based on multispecies-equilibria and therefore account for non-trivial effects of indirect interactions and HOIs on species persistence [20], [36], [37]. Furthermore, the - map could complement other multispecies approaches such as the cavity method by [38]. Because is similar to a measure of the average interaction strength of species [39], we hypothesize that the across species mean is related to interaction antagonism, as defined in [38]. Similarly, we expect their heterogeneity and reciprocity to be linked to , as both capture the idea of differences in interaction strength.

Finally, the - map allows simple quantitative cross community comparison. We computed and for a total of 169 two-species plant communities from [15]. For each of these plant communities, densities over time were observed, to which a Lotka-Volterra community model was fitted. This allowed us to compute and (Figure 4C), which reveals that most investigated communities have negative frequency dependence (), confirming the results from [15]. There has been some exploration of communities under positive frequency dependence () but there is virtually no exploration of ecological communities with in MCT, but see [31], suggesting that persistence in many community types presenting positive interactions has remained unexplored.

**Mapping and 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, for instance, that direct environmental changes such as those caused by global change drivers can affect species persistence in negative and positive ways, leading some species to extinction while increasing the abundance of others [40]. To understand why this variation among species occurs we need an approach that quantifies persistence, and its causes, across species.

Environmental changes can affect both the intrinsic ability of species to grow in the absence of interactions and species interactions. Both types of modifications can lead to changes of both and (see Box 2). Thus, - mapping allows a universal understanding of how species persistence changes as a result of the aforementioned high-level processes. With this approach we can define when a species cannot persist due to *environmental filtering*, that is a negative intrinsic growth rate, , or due to changes in the sign, strength, and presence [41] of species interactions that occur along broad environmental change (e.g. nutrient enrichment [42], warming [43], drought and cold [44], or environmental pollution [45]). Additionally, the - map gives not only qualitative information about persistence (yes or no), but also quantitative information (e.g. how close a species is to the persistence line). In cases where the invasion growth rate holds quantitative information about persistence [46]–[48], species that are closer to the persistence line will be more sensitive to extinction through environmental change (but see limitations).

Connecting shifts of species interactions with persistence has only recently started [49], for example using species pairs of yeast [12] and annual plants [17], [50]. The proposed framework can foster such studies as it provides a common framework that is applicable to various taxa and systems 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 5A) and more complex ecological communities (Figure 5B). For illustration, we assume that environmental change causes an absolute increase in species interactions, and a decrease in species’ intrinsic growth rates for the communities in Figure 4A. 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 [51], [52]. However, we want to emphasize that this specific environmental change is purely theoretical and chosen for illustration purposes only. Empirical examples of environmental effects on niche and fitness differences can be found elsewhere [17], [53]. Our illustrations show that weakening, and potentially even sign-switching, of species interactions can qualitatively change the location of species within the - map (Figure 5A and 5B). For example, the specific environmental change used here transforms priority effects (Figure 4A “priority effects”) into the classic case of two competing and coexisting species, e.g. resource competition (Figure 5A “resource competition”), where species persist when negative frequency dependence () is strong enough to overcome differences in competitive ability (). Likewise, the specific environmental change used here transforms “facilitation-competition” (Figure 4A) into “mutualism” (Figure 5A) because the specific environmental change used here makes species interactions both positive and therefore symmetric in sign. Finally, in a mutualistic community (Figure 4A, “mutualism”), environmental change makes the persistence of one species only possible in the presence of the other community members (Figure 5A, “obligate mutualism”). The specific environmental change used here 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 ). Finally, for the mutualistic network model (Figure 5B), we assume an environmental change driver increases the mortality of the pollinators (e.g. a pesticide). Importantly, we here assume that this environmental change does not affect the interaction matrix, but only the intrinsic growth rates, yet this environmental change indirectly affects the location of all species in the - map. Importantly, all plant species now experience a net negative effect of species interactions.

Taken together, these illustrations highlight that the - map allows understanding the expected consequence of environmental change for species persistence. Other approaches to understand species persistence, such as structural stability, are also suited to address this question [54]. In addition, the - map offers two novelties. First, it is both species-specific [8], [20] and provides community-level information because all and depend on the and 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. Second, the - map allows to identify specific persistence processes. It therefore unveils which of the three high level processes or their combination are affected by environmental change. Different environmental changes may act very differently but still have identical effects on persistence and species richness. For example, decreased precipitation may increase competition for water and therefore switch species interactions from facilitative to competitive. Increased temperature may reduce the intrinsic fitness of a species such that it can no longer grow, even in the absence of species interactions. The - map will allow to discern how these environmental changes affect the persistence of each species within a community.

**Mapping and 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 [55]. 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 [56]. 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 [57], [58]. Yet, most available approaches rely on indirect comparisons, i.e. they examine to what extent models match data collected in different communities [59], [60]. The - 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 - map provides common currency across ecological disciplines [61], 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 or the combination of both) is driven by the same high-level processes or not. Another question deals with the evolution of species interactions, asking if phylogeny [9], [21] or evolutionary-constrained traits [62], e.g. size and feeding role, predict - mapping across contrasting taxonomic groups, e.g. plants, plankton, and vertebrates [63], [64]. Addressing such questions will facilitate across-community comparisons, which allows examining how the complexity of interaction types and the architecture of species interactions affects the dynamics of ecological communities and their maintenance.

**Why should one compute and ?**

and are based on three key growth rates of species, the intrinsic growth rate , the invasion growth rate and the no-niche growth rate (Box 2). Computing and from these growth rates does not add any additional information, for example the inequality is equivalent to . Why then should one compute and , as opposed to just investigate and ? We reidentify three reasons.

1. The - map visualizes which high-level processes drive community dynamics. Conversely, combining the three growth rates into look-up tables or 3 dimensional graphs would not aid communication and thus obscure ecological interpretation.

2. The - map tracks the effect of environmental changes into two axis which are potentially orthogonal or independent ([8], [9] but see [65]). Effects of environmental change are therefore easily appreciable as, for instance, primarily reducing the competitive strength of a species (increase in ). Conversely, a decrease of all three growth rates and would need to be observed to conclude the same decrease in competitive strength. We therefore expect and to be more interdependent than and .

3. The - map is scaling invariant and therefore allows comparisons between communities. Conversely, the growth rates depend very much on the species properties. Changing the time variable from days to hours would directly scale all growth rates and therefore make comparisons among communities very difficult. Similarly, we expect trees to have much lower growth rates than phytoplankton [66], which again would hamper community comparisons. Conversely, and are both normalised such that any scaling of the form , e.g. temporal scaling or allometric scaling, does not affect or (see Appendix 5)

**Limitations**

Assessing persistence directly is challenging [67]–[70]. MCT has traditionally assessed persistence through “invasion analysis”, which tests whether all species in a community are able to increase in abundance when rare [7], [71], [72]. Because it is an extension of MCT, - mapping inherits all the limitations of invasion analysis. These limitations include the fact that, in some community types, the requirement of a positive invasion growth rate can be a too stringent criterion for persistence, and that invasion analysis is technically impossible [36], [37], [73]. The latter point may become especially problematic in species rich communities [74]. Despite all these limitations, invasion growth rates remain widely used in coexistence theory [48], [61], [72], [75]–[77]. - mapping does not offer a new method to assess coexistence, but focuses on the interpretation of coexistence. That is, if one has already verified that invasion analysis can be applied, then - mapping can help interpret the outcome of coexistence via the occurrence of the three higher level processes.

The most prominent limitation of invasion analysis is that it can only be applied when the sub-communities (the ones without the invader) represent a stable equilibrium [78], [79]. Numerical simulations or direct computation can easily verify if this is the case for each of the sub-communities. If invasion analysis is possible it may incorrectly predict coexistence and there are no general guidelines on when invasion analysis correctly predicts coexistence [68], [80]. However, a recent study has shown when invasion analysis is applicable it mostly correctly predicts coexistence [39].

In communities where invasion analysis is both possible and useful, a second limitation may emerge. That is, measuring and can be labour-intensive, especially in species-rich communities. For a two-species community, one option is to empirically measure different kinds of growth rates (see Box 2 for the three growth rates that define and ). This will, however, be unfeasible for a multi-species community. A more feasible approach to apply this method to a multispecies community is therefore to parameterize a community model [81]–[83] and derive and either analytically or through simulations. Both approaches (empirically measuring growth rates and parameterizing models) are potentially labour-intensive and various trade-offs emerge regarding the model complexity that is appropriate to represent the system considered [84]. Note however, that this limitation is a limitation to essentially all approaches that assess persistence [72], [78]. Finally, as with any empirical estimation of niche and fitness differences, successfully observing effects of species or community identity, or of environmental conditions, on and depends on how precisely one can measure abundances. Unfortunately, measurements of niche and fitness differences yield relatively large uncertainties in general, independent of which method is used [12], [32], [85].

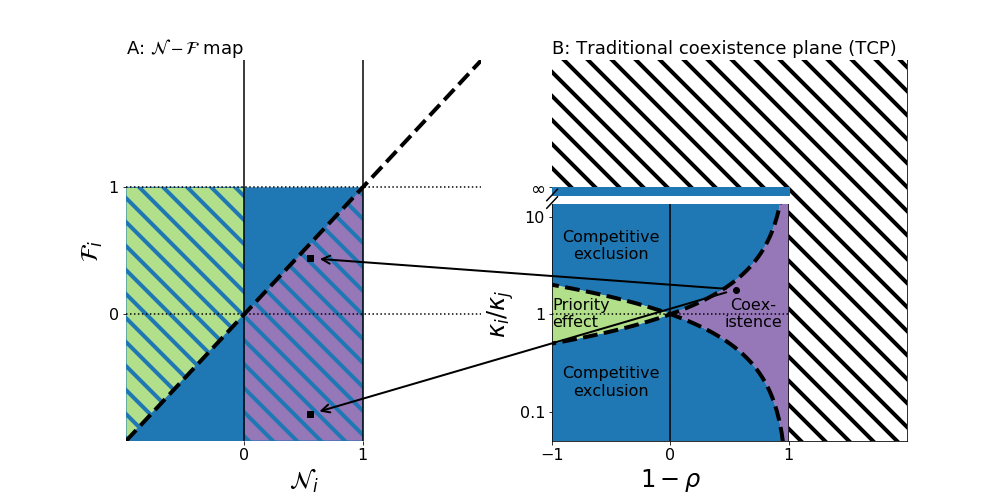
**Conclusions**

We propose a framework that extends MCT beyond competition and embraces the myriad of species interactions that occur in nature. This framework is based on a redefinition of niche and fitness differences as species-specific characteristics rather than as community characteristic. By mapping niche and fitness differences, we can further evaluate which high-level processes underpin persistence (Box 2). These high-level processes in essence reflect how species persistence depends on and .

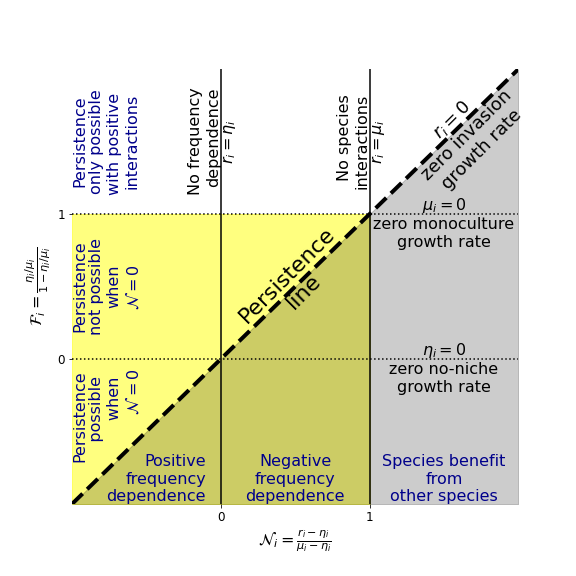
The second innovation of this framework is that it goes beyond predictions of coexistence for species pairs. This is because the approach here presented summarizes the effect that many species interactions can have on persistence. This common framework represents an unprecedented opportunity to examine how multiple interaction types, including direct pairwise, indirect interaction chains and HOIs, in various ecological communities contribute to the maintenance of biodiversity.

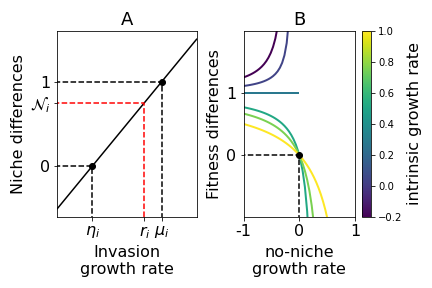
Finally, because variation in environmental conditions affect the ability of species to grow and the way species interact, we can inspect with this framework, via estimations of niche () and fitness differences (), whether and how changes in environmental conditions have a positive or negative effect on species persistence, and therefore, on community properties such as species richness and composition.

The - map connects the history and the future of MCT. It includes previously described cases of the theory (competing species pairs, Figure 1B), while uncovering new regions that represent other interaction types, yielding insights that were previously unknown (Figure 1A). Which kind of communities would represent these previously unexplored regions is a new research field awaiting exploration. We believe this exploration can trigger collaboration between different sub-disciplines in ecology, most notably among different groups of empiricists interested in positive and negative interactions occurring within and between trophic levels. Nature contains different types of ecological communities with disparate species interaction networks. Potentially different types of ecological communities may lead to similar - mapping, showing that - despite these differences - the same high-level processes drive persistence. Finally, we believe that formalising species interactions with the - map will also foster collaboration between theoreticians and empiricists because mapping is not model-specific and may even be applied to empirically measured growth rates. As such, the - map offers a standardised way to compare empirical and theoretical results. Overall, our framework illustrates how simple definitions of the determinants of species persistence create a reference system that applies to many communities composed of species with different interaction types.

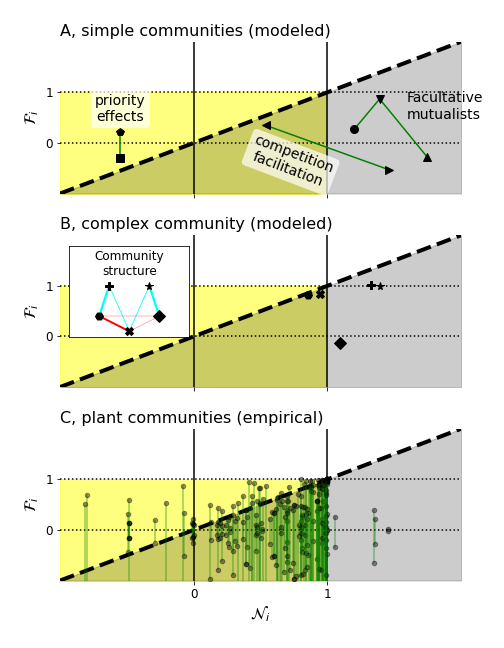


**Figure 1:** The - map (A) differs from the traditional coexistence plane (TCP, B, adapted from Ke and Letten 2018). First, the TCP locates communities (black dot), while the - map locates species (black squares). The two squares (A) correspond to the two species from the black-dot-community (B). Thus, 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 () or species with negative intrinsic growth rates (“”, but strictly speaking is undefined), as indicated by the black-white hatched region. Instead, - mapping will locate species with such properties in the white region.

**Figure 2:** Niche and fitness differences allow positioning each species in the niche and fitness differences map (- map). The map is unbounded in all four directions to infinity and is divided into different regions by five lines (black text). The diagonal line is the persistence line (), below which species are assumed to persist (, shaded area), and above which species may go extinct (). The other four lines divide both niche and fitness differences into three mutually exclusive and qualitatively different sections (blue text), leading to a total of nine different regions in the - map (See Box 2 for specific details and Appendix 4 for mathematical proofs).

****

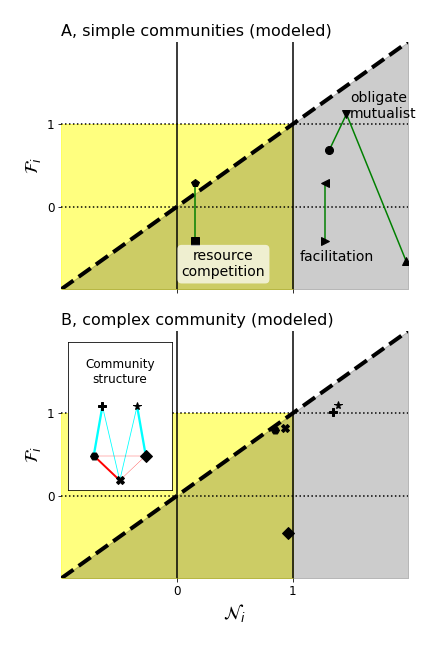
**Figure 3: A**: Niche differences can be seen as an inter- or extrapolation of the invasion growth rate . The nodes of the interpolation are defined by the no-niche growth rate and the intrinsic growth rate , which map to 0 and 1 respectively. However, in general these three growth rates are interdependent, such that changing the interpolation location would also affect its nodes. B: Fitness differences as a function of the no-niche growth rate for different intrinsic growth rates (color). Fitness differences are 0 when the no niche growth rate is 0, independent of the intrinsic growth rate (black dot). Similarly, fitness differences are 1 when the intrinsic growth rate is 0, independent of the no-niche growth rate (blue line). When approaches the fitness differences diverge to positive () or negative infinity (), as by assumption. For the special case of the line stops at .



**Figure 4:** - 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 2. A: Three examples of simple communities with different kinds of species interactions. Markers represent species, connections represent direct interactions. All three communities follow Lotka-Volterra dynamics (), where is the vector of intrinsic growth rates and A is the interaction matrix representing different interaction types: priority effects , competition-facilitation , and facultative mutualists . See Appendix 2 to compute and for multispecies Lotka-Volterra communities.

B: An example of a mutualistic network containing three plants (dot, cross and diamond) and two pollinators (plus and star); The inset shows direct species interactions and their relative strength, red illustrates competitive interactions and blue illustrates mutualistic interactions. Importantly, the position of each species depends on all its direct *and* indirect interactions with other species. All plant species have both positive and negative interspecific interactions, yet only one plant species benefits from those interactions (diamond, ).

C: - mapping of 169 empirical two-species plant communities, taken from a recent review [15], with dots and connections as in the other panels. We converted the original and from [15] to the definition as defined in Box 2. This panel shows that most studies have experimentally investigated communities with and ; there has been some exploration of communities under positive frequency dependence () but there is virtually no exploration of ecological communities with in MCT, but see [31], suggesting that persistence in many community types that present positive interactions has remained unexplored.



**Figure 5:** - mapping can help understand the effects of environmental change on persistence. A: The communities from Figure 4A 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: , mutualism , obligate mutualism . The new intrinsic growth rates are , except for the obligate mutualism community, in which it is B: The community from Figure 4B was exposed to an environmental change driver (e.g. a pesticide) that increases the mortality of the pollinators, but does not affect the species interactions, nor the growth rates of the plants. This environmental change driver indirectly affects the plants such that no plant benefits from species interactions (). Importantly, this illustrates that changes in growth rates may affect in multispecies communities. Species markers from 5A and B correspond to species markers from 4A and B.

|  |
| --- |
| **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 (), the opposite of niche overlap (), have been conceptualised as the dissimilarity of the consumption vectors of two species [86], [87]. Niche differences of 0 meant the consumption vectors are identical, while niche differences of 1 meant that species do not consume common resources. Intermediate cases meant species limit themselves more than they limit others, i.e. interspecific interactions are less negative than intraspecific interactions [8]. Consequently, negative niche differences were interpreted as weaker intraspecific interactions than interspecific interactions, which corresponds to positive frequency dependence [22], [88], [89].  Apart from niche differences, fitness differences are needed to assess the outcome of species interactions [7]. Fitness differences measure the difference in inherent competitive strength between both species if niche differences would be absent [8]. For two competitors to coexist, niche differences must overcome fitness differences. If both species perform equally well, the fitness differences of both species are 1, but other definitions chose 0 for equal performance [16], [20].  Recent developments in MCT have led to three main insights [8], [20]. First, while niche and fitness differences have been traditionally considered community properties (above text and Figure 1B), this is only true for the specific case of competing species pairs. In virtually all other community types, niche and fitness differences should be species properties [8], [20]. In a multispecies community, niche differences describe how much the niche of a focal species differs from the rest of the community. Fitness differences compare the fitness of the focal species to the rest of the community. Second, niche differences can exceed 1, where they indicate positive interspecific interactions, e.g. facilitation [90] or predation (Figure 4A and B). Third, as we show here, species with negative intrinsic growth rates have lower fitness and therefore higher fitness differences than species with zero intrinsic growth rate, e.g. obligate mutualists or predators (Figure 5A and B). Fitness differences exceeding 1 indicate negative intrinsic growth rate.  Traditional niche differences () and fitness differences () are defined only for competitive two species communities. The new niche () and fitness differences () as proposed here and in [20] can be applied to a much larger range of communities. Most importantly, and are community properties, while and are species properties, i.e. and are niche and fitness differences of species (Figure 1). |

|  |
| --- |
| **Box 2: How niche and fitness differences reveal high level processes**  We define niche and fitness differences according to [20]. For the focal species we first define and mathematically for a community in which the per-capita growth rate of species *i*, , depends on species *i*’s density and on that of the other species: , where is the vector only containing the densities of the other species. For such a community we define the intrinsic growth rate the invasion growth rate and the no-niche growth rate , where is the equilibrium density of species in the resident community without species , and is a conversion factor that converts densities of species to densities of species . We assume that , which excludes strong Allee effects, as is usually done in modern coexistence theory [80], [91]. Invasion by definition hinges on the capacity of species to realise growth at low abundance, consequently, assessing coexistence with invasion growth rates in a community driven by Allee effects is potentially not possible. For simplicity we assume that a point equilibrium exists, however, the theory also applies to an equilibrium distribution by taking average growth rates over the equilibrium distribution.  The conversion factors ensure that the total species density at invasion () and the species density at the no-niche growth rate () are the same, which allows the proper assessment of frequency dependence. The appendix contains a mathematical definition of the conversion factors.  We then define and as:  These definitions, by design, align with the observations from box 1. Computer code in R and python is available to compute and as well as the conversion factors : https://github.com/juergspaak/NFD\_definitions . We note that the definition of differs slightly from the original ones [20] to facilitate visualisation on the - map, as discussed below. We also want to caution that our interpretation differs from other measures of fitness, yet it is consistent with what is usually described as fitness in the modern coexistence theory [7], [8].  The numerator of compares two growth rates of species with the same scaled total density, but different frequencies of the focal species (0% in ; 100% in ), it therefore assesses frequency dependence. The denominator on the other hand compares two growth rates of species with the same frequency of species (100%) but with different densities, it therefore assesses density dependence. therefore measures the normalised frequency dependence of species .  The no-niche growth rate measures the growth rate of species in the hypothetical case where there are no niche differences, which is in essence the fitness of species . The scaling by ensures that we can compare fitness differences from different communities. We take the negative of the original definition from [20] and divide by to obtain Eq.2 such that the fitness differences depend continuously on the intrinsic growth rate , as explained in the Appendix 3, Figure S3. The invasion growth rate quantifies if species can persist (positive invasion growth rates, ), or not (negative invasion growth rates, ). The persistence line (Figure 2) separates these two cases.  The intrinsic growth rate measures growth in absence of other species and thus tells which species survive in monoculture (, see Figure 3B), e.g. basal species relying on abiotic resources. Species with negative intrinsic growth rates () 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 (, see Figure 3B) persist in the absence of niche differences. Species with negative no-niche growth rates () 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 (, Figure 3A), e.g. because of priority effects [22]. Conversely, species with negative frequency dependence (), grow faster when rare. Finally, species with an invasion growth rate that exceeds their intrinsic growth rate () grow faster in a community than when alone. Examples include predators and mutualists.  These definitions of niche and fitness differences lead to essentially equivalent expressions as the traditional definitions for a competitive two-species Lotka Volterra model ( and for the traditional niche overlap and fitness differences from [92]). and . The general expressions for multispecies, non-competitive Lotka-Volterra models can be found in the Appendix 3. |

|  |
| --- |
| Glossary   * Species persistence: A species persists in a given environment if it avoids local extinction in the long-term, despite varying its population density over time. We here assume that this is equivalent to the ability to invade when rare (positive invasion growth rate). * Species coexistence: The species of a community are said to coexist if all species persist. * Environmental filtering: Environmental conditions can limit the presence of species at a given location. This occurs when species in the absence of interactions cannot maintain positive population growth and therefore has a fitness difference above 1. * Niche differences: Describe how much the limiting factors of a species differ from the limiting factors of the other species. Positive niche differences stabilize the population dynamics of interacting species, negative niche differences destabilize population dynamics. * Fitness differences: Fitness differences correspond to the growth rates of a species in the absence of all niche differences, it relates to a species intrinsic capacity to survive and how much it a species limits its own growth rate. A highly competitive species has a low fitness difference. * Priority effects: When the arrival order of species affects the community composition. When a species experiences positive frequency-dependent growth rates, they limit the other species more than itself. As a consequence, the first species to arrive can dominate, assuming that fitness differences are not too strong. * Density dependence: The density dependence of a species growth rate is how sensitive the species growth rate reacts to changes in total density. Most notably we here define it as the difference between the intrinsic growth rate and the no-niche growth rate * Frequency dependence: The frequency dependence of a species growth rate is how sensitive the species growth rate is to changes in frequency at constant total density. Most notably, we here define it as the difference between the invasion growth rate and the no-niche growth rate , where the community being invaded has the same total density, but different frequencies. |

References:

[1] D. García-Callejas, R. Molowny-Horas, and M. B. Araújo, “Multiple interactions networks: towards more realistic descriptions of the web of life,” *Oikos*, vol. 127, no. 1, pp. 5–22, 2018, doi: 10.1111/oik.04428.

[2] N. J. B. Kraft, O. Godoy, and J. M. Levine, “Plant functional traits and the multidimensional nature of species coexistence,” *Proc. Natl. Acad. Sci.*, vol. 112, no. 3, pp. 797–802, 2015, doi: 10.1073/pnas.1413650112.

[3] O. Godoy, I. Bartomeus, R. P. Rohr, and S. Saavedra, “Towards the Integration of Niche and Network Theories,” *Trends in Ecology and Evolution*, vol. 33, no. 4. 2018. doi: 10.1016/j.tree.2018.01.007.

[4] S. Kéfi, V. Miele, E. A. Wieters, S. A. Navarrete, and E. L. Berlow, “How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience,” *PLoS Biol.*, vol. 14, no. 8, pp. 1–21, 2016, doi: 10.1371/journal.pbio.1002527.

[5] S. Pilosof, M. A. Porter, M. Pascual, and S. Kéfi, “The multilayer nature of ecological networks,” *Nat. Publ. Group*, vol. 1, no. March, pp. 1–9, 2017, doi: 10.1038/s41559-017-0101.

[6] E. Thébault and C. Fontaine, “Stability of ecological communities and the architecture of mutualistic and trophic networks,” *Science*, vol. 329, no. 5993, pp. 853–856, 2010, doi: 10.1126/science.1188321.

[7] P. Chesson, “Mechanisms of maintenance of speciesdiversity,” *Annu. Rev. Ecol. Evol. Syst.*, vol. 31, 2000.

[8] P. B. Adler, J. HilleRislambers, and J. M. Levine, “A niche for neutrality,” *Ecol. Lett.*, vol. 10, no. 2, pp. 95–104, 2007, doi: 10.1111/j.1461-0248.2006.00996.x.

[9] A. Narwani, M. A. Alexandrou, T. H. Oakley, I. T. Carroll, and B. J. Cardinale, “Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae,” *Ecol. Lett.*, vol. 16, no. 11, pp. 1373–1381, 2013, doi: 10.1111/ele.12182.

[10] S. P. Hart, M. M. Turcotte, and J. M. Levine, “Effects of rapid evolution on species coexistence,” *Proc. Natl. Acad. Sci.*, vol. 116, no. 6, pp. 2112–2117, 2019, doi: 10.1073/pnas.1816298116.

[11] A. I. Pastore, G. Barabás, M. D. Bimler, M. M. Mayfield, and T. E. Miller, “The evolution of niche overlap and competitive differences,” *Nat. Ecol. Evol.*, vol. 5, no. 3, pp. 330–337, Mar. 2021, doi: 10.1038/s41559-020-01383-y.

[12] T. N. Grainger, A. D. Letten, B. Gilbert, and T. Fukami, “Applying modern coexistence theory to priority effects,” *Proc. Natl. Acad. Sci.*, vol. 116, no. 13, pp. 6205–6210, 2019, doi: 10.1073/pnas.1803122116.

[13] O. Godoy, N. J. B. Kraft, and J. M. Levine, “Phylogenetic relatedness and the determinants of competitive outcomes,” *Ecol. Lett.*, vol. 17, no. 7, pp. 836–844, 2014, doi: 10.1111/ele.12289.

[14] S. P. Hart, R. P. Freckleton, and J. M. Levine, “How to quantify competitive ability,” *J. Ecol.*, vol. 106, no. 5, pp. 1902–1909, 2018, doi: 10.1111/1365-2745.12954.

[15] P. B. Adler *et al.*, “Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition,” *Ecol. Lett.*, vol. 21, no. 9, pp. 1319–1329, 2018, doi: 10.1111/ele.13098.

[16] L. Zhao, Q. G. Zhang, and D. Y. Zhang, “Evolution alters ecological mechanisms of coexistence in experimental microcosms,” *Funct. Ecol.*, vol. 30, no. 8, pp. 1440–1446, 2016, doi: 10.1111/1365-2435.12611.

[17] M. D. Bimler, D. B. Stouffer, H. R. Lai, and M. M. Mayfield, “Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency,” *J. Ecol.*, vol. 106, no. 5, pp. 1839–1852, 2018, doi: 10.1111/1365-2745.13030.

[18] C. A. Johnson, “How mutualisms influence the coexistence of competing species,” *Ecology*, vol. 102, no. 6, Jun. 2021, doi: 10.1002/ecy.3346.

[19] C. Chu and P. B. Adler, “Large niche differences emerge at the recruitment stage to stabilize grassland coexistence,” *Ecol. Monogr.*, vol. 85, no. 3, pp. 373–392, 2015, doi: 10.1890/14-1741.1.

[20] J. W. Spaak and F. De Laender, “Intuitive and broadly applicable definitions of niche and fitness differences,” *Ecol. Lett.*, p. doi: https://doi.org/10.1101/482703, 2020, doi: 10.1111/ele.13511.

[21] M. M. Mayfield and J. M. Levine, “Opposing effects of competitive exclusion on the phylogenetic structure of communities,” *Ecol. Lett.*, vol. 13, no. 9, pp. 1085–1093, 2010, doi: 10.1111/j.1461-0248.2010.01509.x.

[22] P. J. Ke and A. D. Letten, “Coexistence theory and the frequency-dependence of priority effects,” *Nat. Ecol. Evol.*, vol. 2, no. 11, pp. 1691–1695, 2018, doi: 10.1038/s41559-018-0679-z.

[23] J. C. D. Terry, J. Chen, and O. T. Lewis, “Natural enemies have inconsistent impacts on the coexistence of competing species,” Ecology, preprint, Aug. 2020. doi: 10.1101/2020.08.27.270389.

[24] T. Fukami, E. Mordecai, and A. Ostling, “A framework for priority effects,” *J. Veg. Sci.*, vol. 27, no. 1, pp. 655–657, 2016, doi: 10.1111/jvs.12434.

[25] C. A. Johnson and J. L. Bronstein, “Coexistence and competitive exclusion in mutualism,” *Ecology*, vol. 100, no. 6, 2019, doi: 10.1002/ecy.2708.

[26] P.-J. Ke and A. D. Letten, “Coexistence theory and the frequency dependence of priority effects,” *biorXiv*, 2018, doi: 10.1101/243303.

[27] T. Fukami, E. A. Mordecai, and A. Ostling, “A framework for priority effects,” *J. Veg. Sci.*, vol. 27, no. 1, pp. 655–657, 2016, doi: 10.1111/jvs.12434.

[28] P. J. Ke and A. D. Letten, “Coexistence theory and the frequency-dependence of priority effects,” *Nat. Ecol. Evol.*, vol. 2, no. 11, pp. 1691–1695, 2018, doi: 10.1038/s41559-018-0679-z.

[29] G. Losapio *et al.*, “Network motifs involving both competition and facilitation predict biodiversity in alpine plant communities,” *Proc. Natl. Acad. Sci.*, vol. 118, no. 6, p. e2005759118, 2021, doi: 10.1073/pnas.2005759118.

[30] O. Godoy and J. M. Levine, “Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory,” *Ecology*, vol. 95, no. 3, pp. 726–736, 2014, doi: 10.1890/13-1157.1.

[31] W. K. Petry, G. S. Kandlikar, N. J. B. Kraft, O. Godoy, and J. M. Levine, “A competition–defence trade-off both promotes and weakens coexistence in an annual plant community,” *J. Ecol.*, vol. 106, no. 5, pp. 1806–1818, 2018, doi: 10.1111/1365-2745.13028.

[32] J. C. D. Terry, J. Chen, and O. T. Lewis, “Natural enemies have inconsistent impacts on the coexistence of competing species,” *J. Anim. Ecol.*, pp. 1365-2656.13534, Jun. 2021, doi: 10.1111/1365-2656.13534.

[33] S. Barot and J. Gignoux, “Mechanisms Promoting Plant Coexistence: Can All the Proposed Processes Be Reconciled ?,” *Oikos*, vol. 106, no. 1, pp. 185–192, 2004.

[34] J. M. Levine, J. Bascompte, P. B. Adler, and S. Allesina, “Beyond pairwise mechanisms of species coexistence in complex communities,” *Nature*, vol. 546, no. 7656, pp. 56–64, 2017, doi: 10.1038/nature22898.

[35] M. M. Mayfield and D. B. Stouffer, “Higher-order interactions capture unexplained complexity in diverse communities,” *Nat. Ecol. Evol.*, vol. 1, no. 3, pp. 1–7, 2017, doi: 10.1038/s41559-016-0062.

[36] S. Saavedra, R. P. Rohr, J. Bascompte, O. Godoy, N. J. B. Kraft, and J. M. Levine, “A structural approach for understanding multispecies coexistence,” *Ecol. Monogr.*, vol. 87, no. 3, pp. 470–486, 2017, doi: 10.1002/ecm.1263.

[37] J. Grilli, G. Barabás, M. J. Michalska-Smith, and S. Allesina, “Higher-order interactions stabilize dynamics in competitive network models,” *Nature*, vol. 548, no. 7666, pp. 210–213, 2017, doi: 10.1038/nature23273.

[38] M. Barbier, J. F. Arnoldi, G. Bunin, and M. Loreau, “Generic assembly patterns in complex ecological communities,” *Proc. Natl. Acad. Sci. U. S. A.*, vol. 115, no. 9, pp. 2156–2161, 2018, doi: 10.1073/pnas.1710352115.

[39] J. W. Spaak, C. Carpentier, and F. De Laender, “Fitness differences, not niche differences, limit species richness,” *bioRxiv*, 2019.

[40] M. Dornelas, N. J. Gotelli, H. Shimadzu, F. Moyes, A. E. Magurran, and B. J. McGill, “A balance of winners and losers in the Anthropocene,” *Ecol. Lett.*, vol. 22, no. 5, pp. 847–854, 2019, doi: 10.1111/ele.13242.

[41] A. Valiente-Banuet *et al.*, “Beyond species loss: The extinction of ecological interactions in a changing world,” *Funct. Ecol.*, vol. 29, no. 3, pp. 299–307, 2015, doi: 10.1111/1365-2435.12356.

[42] W. S. Harpole and D. Tilman, “Grassland species loss resulting from reduced niche dimension,” *Nature*, vol. 446, no. 7137, pp. 791–793, 2007, doi: 10.1038/nature05684.

[43] L. W. Traill, M. L. M. Lim, N. S. Sodhi, and C. J. A. Bradshaw, “Mechanisms driving change: Altered species interactions and ecosystem function through global warming,” *J. Anim. Ecol.*, vol. 79, no. 5, pp. 937–947, 2010, doi: 10.1111/j.1365-2656.2010.01695.x.

[44] A. D. Letten and M. Yamamichi, “Gleaning, fast and slow: in defense of a canonical ecological trade-off,” *Proc. Natl. Acad. Sci.*, vol. 118, no. in press, pp. 1–2, 2021, doi: 10.1073/pnas.2022754118.

[45] J. M. Baert, C. R. Janssen, K. Sabbe, and F. De Laender, “Per capita interactions and stress tolerance drive stress-induced changes in biodiversity effects on ecosystem functions,” *Nat. Commun.*, vol. 7, pp. 1–8, 2016, doi: 10.1038/ncomms12486.

[46] J. Pande, T. Fung, R. Chisholm, and N. M. Shnerb, “Mean growth rate when rare is not a reliable metric for persistence of species,” *Ecol. Lett.*, vol. 23, no. 2, pp. 274–282, 2020, doi: 10.1111/ele.13430.

[47] A. M. Dean and N. M. Shnerb, “Stochasticity-induced stabilization in ecology and evolution: a new synthesis,” *Ecology*, vol. 101, no. 9, pp. 1–14, 2020, doi: 10.1002/ecy.3098.

[48] S. P. Ellner, R. E. Snyder, P. B. Adler, G. Hooker, and S. J. Schreiber, “Technical Comment on Pande et al. (2020): Why invasion analysis is important for understanding coexistence,” *Ecol. Lett.*, 2020, doi: 10.1111/ele.13580.

[49] S. Cenci, A. Montero-Castaño, and S. Saavedra, “Estimating the effect of the reorganization of interactions on the adaptability of species to changing environments,” *J. Theor. Biol.*, vol. 437, pp. 115–125, 2018, doi: 10.1016/j.jtbi.2017.10.016.

[50] J. B. Lanuza, I. Bartomeus, and O. Godoy, “Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes,” *Ecol. Lett.*, vol. 21, no. 6, pp. 865–874, 2018, doi: 10.1111/ele.12954.

[51] F. De Laender *et al.*, “Reintroducing Environmental Change Drivers in Biodiversity–Ecosystem Functioning Research,” *Trends Ecol. Evol.*, vol. 31, no. 12, pp. 905–915, 2016, doi: 10.1016/j.tree.2016.09.007.

[52] F. T. Maestre *et al.*, “Plant species richness and ecosystem multifunctionality in global drylands,” *Science*, vol. 335, no. 6065, pp. 214–218, 2012, doi: 10.1126/science.1215442.

[53] L. Matías, O. Godoy, L. Gómez-Aparicio, and I. M. Pérez-Ramos, “An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks,” *J. Ecol.*, vol. 106, no. 3, pp. 826–837, 2018, doi: 10.1111/1365-2745.12962.

[54] C. Song, R. P. Rohr, and S. Saavedra, “A guideline to study the feasibility domain of multi-trophic and changing ecological communities,” *J. Theor. Biol.*, vol. 450, pp. 30–36, 2018, doi: 10.1016/j.jtbi.2018.04.030.

[55] J. A. Lawton, “Are there general laws in ecology?,” *Oikos*, vol. 84, no. 2, pp. 177–192, 1999.

[56] M. Vellend, *The theory of ecological communities*. Princeton University Press, 2016.

[57] S. R. Carpenter *et al.*, “Accelerate Synthesis in Ecology and Environmental Sciences,” *BioScience*, vol. 59, no. 8, pp. 699–701, 2009, doi: 10.1525/bio.2009.59.8.11.

[58] T. Poisot, R. LaBrie, E. Larson, A. Rahlin, and B. I. Simmons, “Data-based, synthesis-driven: Setting the agenda for computational ecology,” *Ideas Ecol. Evol.*, vol. 12, pp. 9–21, 2019, doi: 10.24908/iee.2019.12.2.e.

[59] R. S. Etienne *et al.*, “A minimal model for the latitudinal diversity gradient suggests a dominant role for ecological limits,” *Am. Nat.*, vol. 194, no. 5, pp. E122–E133, 2019, doi: 10.1086/705243.

[60] J. M. K. Rip and K. S. Mccann, “Cross-ecosystem differences in stability and the principle of energy flux,” *Ecol. Lett.*, vol. 14, no. 8, pp. 733–740, 2011, doi: 10.1111/j.1461-0248.2011.01636.x.

[61] T. N. Grainger, J. M. Levine, and B. Gilbert, “The Invasion Criterion: A Common Currency for Ecological Research,” *Trends Ecol. Evol.*, vol. 34, no. 10, pp. 925–935, 2019, doi: 10.1016/j.tree.2019.05.007.

[62] R. M. Germain, J. T. Weir, and B. Gilbert, “Species coexistence: Macroevolutionary relationships and the contingency of historical interactions,” *Proc. R. Soc. B Biol. Sci.*, vol. 283, no. 1827, 2016, doi: 10.1098/rspb.2016.0047.

[63] I. M. Pérez-Ramos, L. Matías, L. Gómez-Aparicio, and Ó. Godoy, “Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions,” *Nat. Commun.*, vol. 10, no. 1, pp. 1–11, 2019, doi: 10.1038/s41467-019-10453-0.

[64] I. Gallego, P. Venail, and B. W. Ibelings, “Size differences predict niche and relative fitness differences between phytoplankton species but not their coexistence,” *ISME J.*, 2019.

[65] C. Song, G. Barabás, and S. Saavedra, “On the consequences of the interdependence of stabilizing and equalizing mechanisms,” *Am. Nat.*, pp. 000–000, 2019, doi: 10.5061/dryad.nk1d456.1.

[66] N. Marba, C. M. Duarte, and S. Agusti, “Allometric scaling of plant life history,” *Proc. Natl. Acad. Sci.*, vol. 104, no. 40, pp. 15777–15780, Oct. 2007, doi: 10.1073/pnas.0703476104.

[67] J. Huisman and F. J. Weissing, “Biodiversity of plankton by species oscillations and chaos,” *Nature*, vol. 402, no. 6760, pp. 407–410, 1999, doi: 10.1038/46540.

[68] S. J. Schreiber, “Criteria for Cr robust permanence,” *J. Differ. Equ.*, vol. 162, no. 2, pp. 400–426, 2000, doi: 10.1006/jdeq.1999.3719.

[69] A. T. Clark, H. Hillebrand, and W. S. Harpole, “Scale both confounds and informs characterization of multi-species coexistence in empirical systems,” *Am. Nat.*, no. May, p. 705826, 2019, doi: 10.1086/705826.

[70] S. J. Schreiber, *Coexistence in the Face of Uncertainty*, vol. 79. 2017. doi: 10.1007/978-1-4939-6969-2.

[71] P. Chesson, “Multispecies Competition in Variable Environments,” *Theor. Popul. Biol.*, vol. 45, no. 3, pp. 227–276, 1994, doi: 10.1006/tpbi.1994.1013.

[72] S. P. Ellner, R. E. Snyder, P. B. Adler, and G. Hooker, “An expanded modern coexistence theory for empirical applications,” *Ecol. Lett.*, 2019, doi: 10.1111/ele.13159.

[73] G. Barabás, R. D’Andrea, and S. M. Stump, “Chesson’s coexistence theory,” *Ecol. Monogr.*, vol. 88, no. 3, pp. 277–303, 2018, doi: 10.1002/ecm.1302.

[74] J. M. Levine, J. Bascompte, P. B. Adler, and S. Allesina, “Beyond pairwise mechanisms of species coexistence in complex communities,” *Nature*, vol. 546, no. 7656, pp. 56–64, 2017, doi: 10.1038/nature22898.

[75] A. D. Letten, M. K. Dhami, P. J. Ke, and T. Fukami, “Species coexistence through simultaneous fluctuation-dependent mechanisms,” *Proc. Natl. Acad. Sci. U. S. A.*, vol. 115, no. 26, pp. 6745–6750, 2018, doi: 10.1073/pnas.1801846115.

[76] S. P. Ellner, R. E. Snyder, and P. B. Adler, “How to quantify the temporal storage effect using simulations instead of math,” *Ecol. Lett.*, vol. 19, no. 11, pp. 1333–1342, 2016, doi: 10.1111/ele.12672.

[77] P. Chesson, “Quantifying and testing coexistence mechanisms arising from recruitment fluctuations,” *Theor. Popul. Biol.*, vol. 64, no. 3, pp. 345–357, 2003, doi: 10.1016/S0040-5809(03)00095-9.

[78] S. Saavedra, R. P. Rohr, J. Bascompte, O. Godoy, N. J. B. Kraft, and J. M. Levine, “A structural approach for understanding multispecies coexistence,” *Ecol. Monogr.*, vol. 87, no. 3, pp. 470–486, 2017, doi: 10.1002/ecm.1263.

[79] J. Grilli, G. Barabás, M. J. Michalska-Smith, and S. Allesina, “Higher-order interactions stabilize dynamics in competitive network models,” *Nature*, vol. 548, no. 7666, pp. 210–213, 2017, doi: 10.1038/nature23273.

[80] G. Barabás, R. D’Andrea, and S. M. Stump, “Chesson’s coexistence theory,” *Ecol. Monogr.*, vol. 88, no. 3, pp. 277–303, 2018, doi: 10.1002/ecm.1302.

[81] F. Carrara, A. Giometto, M. Seymour, A. Rinaldo, and F. Altermatt, “Inferring species interactions in ecological communities: a comparison of mehtods at different levels of complexity,” *Methods Ecol. Evol.*, no. 6, pp. 895–906, 2015.

[82] D. S. Maynard, J. T. Wootton, C. A. Serván, and S. Allesina, “Reconciling empirical interactions and species coexistence,” *Ecol. Lett.*, vol. 22, no. 6, pp. 1028–1037, 2019, doi: 10.1111/ele.13256.

[83] J. M. Baert, C. R. Janssen, K. Sabbe, and F. De Laender, “Per capita interactions and stress tolerance drive stress-induced changes in biodiversity effects on ecosystem functions,” *Nat. Commun.*, vol. 7, pp. 1–8, 2016, doi: 10.1038/ncomms12486.

[84] A. T. Clark *et al.*, “Predicting species abundances in a grassland biodiversity experiment: Trade‐offs between model complexity and generality,” *J. Ecol.*, no. October, pp. 1365-2745.13316, 2019, doi: 10.1111/1365-2745.13316.

[85] J. W. Spaak, “Reinterpretation of niche and fitness differences improves our understanding of species coexistence,” University of Namur, 2020.

[86] P. Chesson, “MacArthur’s consumer-resource model,” *Theor. Popul. Biol.*, vol. 37, no. 1, pp. 26–38, 1990, doi: 10.1016/0040-5809(90)90025-Q.

[87] S. H. Hurlbert, “The Measurement of Niche Overlap and Some Relatives,” *Ecology*, vol. 59, no. 1. pp. 67–77, 1978. doi: 10.2307/1936632.

[88] T. Fukami, E. A. Mordecai, and A. Ostling, “A framework for priority effects,” *J. Veg. Sci.*, vol. 27, no. 1, pp. 655–657, 2016, doi: 10.1111/jvs.12434.

[89] E. A. Mordecai, “Pathogen impacts on plant communities: unifying theory, concepts, and empirical work,” *Ecol. Monogr.*, vol. 81, no. 3, pp. 429–441, 2011.

[90] T. Koffel, T. Daufresne, and C. A. Klausmeier, “From competition to facilitation and mutualism: a general theory of the niche,” *Ecol. Monogr.*, p. ecm.1458, Apr. 2021, doi: 10.1002/ecm.1458.

[91] S. J. Schreiber, M. Yamamichi, and S. Y. Strauss, “When rarity has costs : coexistence under positive frequency-dependence and environmental stochasticity,” *biorXiv*, no. 2, pp. 1–28, 2017, doi: https://doi.org/10.1101/161919.

[92] P. Chesson, S. Pacala, and C. Neuhauser, “10. Environmental Niches and Ecosystem Functioning,” in *The Functional Consequences of Biodiversity*, D. Tilman, A. P. Kinzig, and S. Pacala, Eds. Princeton University Press, 2013, pp. 213–245. doi: 10.1515/9781400847303.213.