Niche difference determines coexistence and similar underlying processes in four ecological groups

Running Title:Metaanalysis of niche and fitness differences

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Abstract

Understanding how species interactions affect community composition is an important objective in ecology. Yet, the multitude of methods to study coexistence has hampered cross-community comparisons. Here, we standardized niche and fitness differences across 1018 species pairs to compare the processes driving composition and outcomes, among four community types (annual plant, perennial plant, phytoplankton, and bacteria/yeast). First, we show that niche differences are more important drivers of coexistence than fitness differences. Second, in all community types negative frequency dependence is the most frequent process. Finally, the outcome of species interactions differs among community types. Coexistence was the most frequent outcome for perennial plants and phytoplankton, while competitive exclusion was the most prevalent outcome in annual plants and bacteria/yeasts. Overall, our results show that niche and fitness differences can be used as a common currency that allow cross community comparisons to understand species coexistence.

Keywords— Coexistence theory, Meta-analysis, Persistence, Community types, Species interactions

1 Introduction

Species interact in a variety of ways. Quantifying the consequences of such interactions for the capacity of species to coexist and form communities is a central objective in ecology (Chesson, 2000a; Barabás, D'Andrea, et al., 2018; Saavedra et al., 2017; Spaak, Godoy, et al., n.d.). One challenge is that, even at a local scale, the diversity of potential mechanisms is overwhelming and difficult to track (Pilosof et al., 2017). However, while species can physically interact via an unlimited number of mechanisms, these interactions can only result in no more than three fundamental processes: positive frequency dependence, negative frequency dependence, and facilitation (Spaak and De Laender, 2020). All of these processes quantify how species grow in the presence of heterospecifics. Positive frequency dependence refers to species growing slower when rare, i.e. when at low frequency. This process can emerge when, for example, species mostly consume resources that are least limiting to their growth (Ke and Letten, 2018; Fukami et al., 2016). Negative frequency dependence is arguably the best-known process, occurring when species grow faster when at low frequency. This process can be driven by mechanisms such as resource partitioning (Tilman, 1982), or by spatial or temporal variation of environmental conditions (Sears and Chesson, 2007; Usinowicz et al., 2012; Tan et al., 2017). Facilitation, finally, occurs when species grow better in presence of

heterospecifics than when alone. Again, a large array of specific mechanisms can give rise to this process, including the use of other species' exudates in diatom algae (Vanelslander et al., 2009), or the amelioration of harsh environmental conditions by neighboring plants (Bruno et al., 2003; Adler, HilleRisLambers, Kyriakidis, et al., 2006; Martorell and Freckleton, 2014; McIntire and Fajardo, 2014).

Species interactions drive three processes, which in turn determine the outcome when an initial set of species starts interacting: coexistence, exclusion, or priority effects. Modern coexistence theory is often based on the principle of invasion fitness (growth at a low frequency) and defines "coexistence" as the situation where each species in a community has positive invasion fitness (Barabás, D'Andrea, et al., 2018). Exclusion or priority effects result in extinction, either independent of or dependent on initial frequencies, respectively (Fukami et al., 2016). Positive frequency dependence is detrimental to coexistence, giving rise to either exclusion or priority effects. Negative frequency dependence leads either to coexistence or exclusion. Facilitation, finally, always leads to coexistence.

Species interactions, the processes they drive, and the resulting outcome are mostly described in case-specific studies, which makes it hard to obtain a synthetic understanding across ecological groups. One could postulate, for example, that communities belonging to a similar type of ecological group (e.g. two annual plant communities) are driven by similar ecological mechanisms and therefore

exhibit similar processes and outcomes. For instance, phytoplankton communities, competing for light, tend to differentiate in their pigment composition which implies lower inter-specific competition, which promotes negative frequency dependence and coexistence (Stomp et al., 2004). Thus, the accumulation of such similar interacting mechanisms should result in a defined ratio of main processes and prevalent outcomes for species belonging to a common ecological group like annual plants. Moreover, ecological groups with similar characteristics, like annual plants and perennial plants may adopt similar mechanisms and ultimately similar distribution of niche and fitness differences.

At present, we lack a synthetic insight into how the diversity of specific mechanisms, observed across a diversity of ecological groups, maps onto the three processes and outcomes. One way to pursue this insight is by applying the concepts of niche and fitness difference across ecological groups (Chesson, 2000b),(Spaak et al. Oikos 2021; Koffel et al 2021). Niche and fitness difference respectively measure how much species limit themselves compared to others, and how competitive ability (e.g. fecundity, dispersion) varies among species (Chesson, 2000b; Barabás, D'Andrea, et al., 2018). Thus, coexistence can occur because niche differences (promote coexistence) are large, or because fitness differences (hamper coexistence) are small. The importance of the former for coexistence has been demonstrated (mostly in plants) in both natural (Adler, Ellner, et al., 2010; Chu

and Adler, 2015; Godoy, Stouffer, et al., 2017; Adler, Smull, et al., 2018; Armitage and Jones, 2019) and experimental communities (Narwani et al., 2013; Mathias and Chesson, 2013; Li Shao-peng et al., 2019). Yet, also small fitness differences have been found to promote coexistence (Chu and Adler, 2015). A first outstanding question is therefore if large niche difference, or small fitness difference, or both, explain coexistence across ecological groups.

Apart from predicting coexistence, niche and fitness differences also tightly link to the three processes driven by species interactions (positive and negative frequency dependence and facilitation) but also predict when exclusion and priority effects occur (Ke and Letten, 2018; Bimler et al., 2018; Picoche and Barraquand, 2020; Spaak, Godoy, et al., n.d.; Koffel et al., 2021). A second question that one could in principle address is therefore if communities belonging to the same ecological group are driven by the same processes and experience the same outcome of species interactions.

Niche and fitness differences can in principle act as a common currency to investigate how species interact (Grainger et al., 2019), and thus address the two outstanding questions cited above. This approach has been applied in the past (e.g.Adler, HilleRisLambers, and Levine, 2007; Godoy, Kraft, et al., 2014; Godoy and Levine, 2014; Narwani et al., 2013), yet comes with an important limitation. That is, the applicability of available definitions is mostly constrained to a limited

set of ecological groups. As a result, different studies use different definitions to study different groups, which hampers cross-community comparisons (Godwin et al., 2020; Spaak and De Laender, 2020). Indeed, different definitions yield different values of niche and fitness differences when computed on the same data, and often carry different units, impeding comparison (Spaak and De Laender, 2020). Only three definitions (Carroll et al. (2011), Zhao et al. (2016), and Spaak and De Laender (2020)) can be applied more widely, enabling the computation of niche and fitness differences for most communities.

Here, we analyze species-interaction data on 1018 species pairs in four ecological groups (phytoplankton, bacteria/yeast, annual and perennial plants) and synthesize the resulting processes and outcomes across ecological groups. While the four ecological groups do not represent the diversity of natural systems, they do represent a variety of life spans, reproduction strategies, and habitats. We first quantified niche and fitness differences using three broadly applicable definitions (Carroll et al. (2011), Zhao et al. (2016), and Spaak and De Laender (2020)) and examined if niche and fitness differences of coexisting species were different from those of non-coexisting species (Figure 1B-C). We tested the hypothesis that niche *and* fitness differences were larger and smaller, respectively, in coexisting pairs, thus jointly promoting coexistence. We then used the definition by Spaak and De Laender (2020) to test if the prevalence of the three main processes and three interaction

outcomes differed among ecological groups. We hypothesized that processes and outcomes would be distinct across ecological groups (Figure 1E-F).

We found that niche differences are consistently a stronger determinant of coexistence than fitness differences, and this result was supported across all four ecological groups. We also found that ecological groups were driven by similar processes, and that negative frequency dependence was the most frequently observed process in all four communities. Ecological groups, however, differed in the prevalence of the interaction outcome. Competitive exclusion was most prevalent in annual plant and bacterial/yeast species, while coexistence was most prevalent in phytoplankton and perennial plant communities. Our results highlight differences and similarities of interaction outcomes and ecological processes across communities.

2 Methods

2.1 Data

We searched the literature for experimental measurements of niche and fitness differences. To do so, we first identified eleven papers that introduce a new definition of niche and fitness differences (See Appendix, Table S5) and gathered all papers that cited one of these eleven original definitions by November 2020.

For the highly cited definitions, superior to 100 citations (Chesson, 2000b; Adler, HilleRisLambers, and Levine, 2007; Chesson and Kuang, 2008), we refined the search with the following keywords: ("niche differences" OR "niche overlap" OR "stabilizing mechanisms") AND ("fitness differences" OR "fitness " OR "equalizing mechanism") AND ("Experiment" OR "Data" OR "Field") AND ("Competition" OR "Coexistence"). Only research-type articles that measured niche or fitness differences experimentally using one of the eleven definitions were considered. Out of the eleven definitions, seven were used empirically (Chesson, 2000b; Carroll et al., 2011; Godoy, Kraft, et al., 2014; Zhao et al., 2016; Saavedra et al., 2017; Bimler et al., 2018; Spaak and De Laender, 2020). We gathered a total of 639 papers, of which 50 contained experimental measurements of niche and fitness differences. These 50 papers contained 29 independent data-sets corresponding to 1018 communities (Appendix, section 6.1, Table.S4). For each article, we extracted all species-specific growth parameters available (competition coefficient, sensitivity, intrinsic growth rate, invasion growth rate, etc.), the taxonomy of the competing species, and the outcome of species interaction, i.e. coexistence, competitive exclusion, or priority effects. This resulted in measured niche and fitness differences in bacteria/yeast (128 communities), phytoplankton (170 communities), annual plants (459 communities), and perennial plants (261 communities).

2.2 Standardizing niche and fitness differences

For the 29 papers collected, the empirically measured niche and fitness differences were computed by different definitions and are therefore not directly comparable (Appendix, section 6.2, Table.S5) (Spaak and De Laender, 2020; Godwin et al., 2020). To compare the different results we first converted them to the same three model-independent definitions of niche and fitness differences (Spaak and De Laender, 2020; Carroll et al., 2011; Zhao et al., 2016). To compute the definition of Carroll et al., 2011 one needs the intrinsic growth rate μ_i and the invasion growth rate r_i of both species. The invasion growth rate is the growth rate of the focal species i when the resident species is at its carrying capacity N_j^*. To compute the definition of Zhao et al., 2016 one needs the invasion growth rate r_i and the carrying capacity N_i^* of both species. To compute the definition of Spaak and De Laender, 2020 one needs the invasion growth rate r_i, the intrinsic growth rate μ_i, and the no-niche growth rate η_i. The no-niche growth rate is the growth rate of species i at the same converted density as species j's equilibrium density. This growth rate can be obtained via simulations. If only the invasion growth rate and the intrinsic growth rates are available, one can produce an estimate of the definition of Spaak and De Laender (2020) (Appendix, section 6.2, Table.S5).

For 719 out of 1018 communities we had a community model, which allows us

to simulate all necessary growth rates as well as the carrying capacity and therefore we computed all 3 definitions for these 719 communities. For 234 out of 299 remaining communities, we found the invasion growth rates and the intrinsic growth rates, but not the carrying capacity nor the no-niche growth rates. For these, we computed only the definitions of Carroll et al., 2011 and estimated the definitions of Spaak and De Laender, 2020. For the remaining 65, we found the invasion growth rates and the carrying capacity, but not the no-niche growth rate nor the intrinsic growth rate. For these we only computed the definition of Zhao et al., 2016.

We use $\mathcal{N}$ and $\mathcal{F}$ to denote niche and fitness differences computed by any of these three methods interchangeably. We shifted the definitions of Carroll et al. (2011) and Zhao et al. (2016) such that a neutral community will have zero $\mathcal{N}$ and zero $\mathcal{F}$ (see Appendix 6.2).

For each definition, we used a two-sample Kolmogorov-Smirnov test (Kolmogoroff and Leontowitsch, 1933) to compare the distribution of $\mathcal{N}$ and $\mathcal{F}$ between coexisting (defined as $\mathcal{N} > \mathcal{F}$) and non-coexisting communities. The two-sample Kolmogorov-Smirnov test verifies if a common probability distribution can be attributed to two sets of data (Press and Teukolsky, 1988).

2.3 Inferring interaction outcomes and underlying processes

One of the key results of modern coexistence theory is that competitive exclusion occurs when fitness differences are too strong to be overcome by niche differences ($\mathcal{N}_i < \mathcal{F}_i$) (Chesson, 2000a; Adler, HilleRisLambers, and Levine, 2007). If niche differences do overcome fitness differences, the sign of niche differences distinguishes between coexistence ($\mathcal{N} > 0$) and priority effect ($\mathcal{N} < 0$) (Ke and Letten, 2018).

$\mathcal{N}$ and $\mathcal{F}$ can therefore be used to distinguish the three possible outcomes of species interactions (coexistence, exclusion, and priority effects). Importantly, these are consistent with the empirically observed outcomes of coexistence.

$\mathcal{N}$ also indicates which processes underpin the outcome of species interactions. Negative $\mathcal{N}$ imply that species limit their competitor more than they limit themselves, also known as positive frequency dependence (Ke and Letten, 2018; Mordecai, 2011). $\mathcal{N}$ between 0 and 1 imply that species limit themselves more than their competitor, also known as negative frequency dependence (Chesson, 2000a; Ke and Letten, 2018). $\mathcal{N}$ larger than 1 imply that species benefit from the presence of the other species, also known as facilitation (Spaak and De Laender, 2020). $\mathcal{N}$ can therefore be used to distinguish three different high-level processes that govern community dynamics.

Given $\mathcal{N}$ and $\mathcal{F}$ by Zhao et al. (2016) one can not predict the outcome of species interactions. Similarly, with the definition of Carroll et al. (2011) we can only predict if coexistence will happen or not. Additionally, these two definitions do not give any insight into the aforementioned higher-level processes, as communities with positive frequency dependence can still have positive $\mathcal{N}$. We, therefore, used the definition of Spaak and De Laender (2020) to measure the prevalence of the three processes (see Appendix, Fig. S1 for the comparison of all three definitions).

2.4 Meta-analyses

To test for differences in the outcomes and processes for different ecological groups, we conduct meta-analyses using the package "metafor" (Viechtbauer, 2010) in R (R Core Team, 2020). With the `escalc()` function, we computed the raw proportion of species pairs for which the different outcomes and processes occur within each study, and the sampling variances of those proportions as its precision. Then, with the `rma.uni()` function, we fitted linear mixed-effects models, with the estimated proportions of the different processes and outcomes as effect sizes and with the community type used as a qualitative moderator. If there are significant differences in the proportions of any of these processes or outcomes for different ecological groups, the moderator associated with some ecological groups will be significantly different to zero, and the fitted mixed model will predict significantly different

proportions for those ecological groups.

To test the robustness of our results, we performed an alternative statistical analysis. This consisted of directly computing the odds ratios of the different processes or outcomes for the different ecological groups considered (see Appendix, section 6.3). Unlike the meta-analysis, this method does not include the original study as random effects.

3 Results

Overall, coexisting communities differed from non-coexisting communities in their niche differences rather than in their fitness differences. Across the four ecological groups (perennial plants, annual plants, phytoplankton, and bacteria/yeast), and regardless of the definition applied, the distributions of fitness difference from communities with coexisting species did not differ significantly from the ones from communities with non-coexisting species in most cases (Fig.2, compare "coexistence" with "no coexistence"). In contrast, niche differences were higher in communities in which species coexist than in communities where species do not. This was true for all ecological groups, and again regardless of the definition applied (Spaak and De Laender, 2020; Carroll et al., 2011; Zhao et al., 2016). The only exception was the case of phytoplankton, analyzed with the definition by Zhao

et al., 2016, where fitness differences were smaller in communities where species coexisted. Taken together, these results support the conclusion that, in our data set, the mechanisms causing niche differences were more important drivers for coexistence than those reducing fitness differences.

Similar processes drove the different ecological groups. Specifically, negative frequency-dependence was the most prevalent process in all four ecological groups (Fig. 3.A), demonstrating the omnipresence of strong self-regulation in all these ecological groups. Roughly 15% of all communities were driven by positive frequency dependence, again across groups. Facilitation was the only process in which the prevalence differed across systems, as it was only present in two of the four groups (perennial plants and phytoplankton). This significant difference can be observed from the moderator values associated with the ecological groups for this process, and from the higher heterogeneity explained by the community type (see Appendix, Table S7).

Despite species interactions leading to similar processes in different groups, the outcome of those interactions differed among groups. Perennial plants resembled phytoplankton communities, while bacterial/yeast communities resembled annual plant communities (Fig.3.B). Coexistence was the most frequent outcome for perennial plants and phytoplankton communities, and this outcome occurred with equal frequency in both ecological groups. In contrast, competitive exclusion was

the most frequent outcome for annual plants and bacteria/yeast, again with equal frequency.

4 Discussion

We used three definitions of niche and fitness differences to compare the main processes resulting from species interactions, and the outcomes of such processes (coexistence, exclusion, priority effects), across four ecological groups. We found that, first, niche differences, rather than fitness differences, explained coexistence across all ecological groups for all three definitions. Second, the same main processes were found to drive the different ecological groups. Negative frequency dependence was the most prevalent process in all groups. Third, the outcome of species interactions differed among ecological groups. Coexistence was the most frequent outcome for perennial plants and phytoplankton, whereas competitive exclusion was most prevalent in annual plant and bacteria/yeast communities.

4.1 Large niche differences, not small fitness differences, explained species coexistence at a local scale

Species coexist when niche differences exceed fitness differences. One could therefore expect that coexisting species have both higher niche differences and lower fitness differences than non-coexisting species. Yet, this hypothesis was rejected as

we only found evidence for the former (Figure 2). At a local scale, coexistence in the examined communities was primarily driven by mechanisms promoting niche differences, e.g. through self-limitation and net positive interactions (Hallett, Farrer, et al., 2018). These results consolidate and expand on findings from primary studies on annual plants (Levine and HilleRisLambers, 2009), perennial plants (Adler, Ellner, et al., 2010; Usinowicz et al., 2012), and phytoplankton (Narwani et al., 2013; Picoche and Barraquand, 2020). Our results show that niche differences are the main determinant for coexistence across ecological groups, highlighting the importance to sustain mechanisms that promote niche differences.

We have focused on species pairs, which by definition contain few species and a single interaction type per pair. We can therefore not be sure that fitness differences would continue to play a minor role for coexistence in communities with more species (Chu and Adler, 2015; Veresoglou et al., 2018; Spaak and De Laender, 2021) inevitably hosting a more diverse set of species interaction types (Parmentier et al., 2020; Bartomeus et al., 2021), including asymmetric and higher-order interactions (Letten and Stouffer, 2019; Levine, Bascompte, et al., 2017; Mayfield and Stouffer, 2017). On the one hand, theory has shown that all else equal, species richness tends to not affect niche differences, while increasing fitness differences (Spaak and De Laender, 2021). This would suggest that the latter will become more important for coexistence in more diverse communities. On the other hand, Godoy, Stouffer, et al.

(2017) have proven the necessity of niche differentiation to permit coexistence in intransitive networks. Hence, a meta-analysis including multispecies communities is needed to explore the extension of our conclusions to more diverse communities.

4.2 Differences and similarities among different ecological groups

Our hypothesis that species interactions in distinct ecological groups translate to different processes was not supported by our results. Instead, negative frequency dependence was prevalent in all ecological groups. Our results align with earlier findings in food web theory showing that negative frequency dependence should be present in up to 90% of interacting species (Barabás, Michalska-Smith, et al., 2017). In annual and perennial plants, intraspecific competition was previously found to be on average 1.5 and four to five times larger than interspecific competition, respectively (Adler, Smull, et al., 2018; Armitage and Jones, 2019). Yet, the prevalence of negative frequency dependence seems to expand beyond annual and perennial plants, across ecological groups, highlighting the importance of self-regulating mechanisms rather than species interspecific differences (Armitage and Jones, 2019). On the other hand, facilitation and positive frequency dependence were significantly less present. Facilitation was nearly absent from annual plant and bacteria/yeast.

The similarity of process across groups is counterintuitive. Annual and perennial

plants are both multicellular organisms subject to similar regulating variables. Some of these regulating variables (e.g. water, nutrient, space (Craine and Dybzinski, 2013)) do not always regulate communities of unicellular microbes in often well-mixed conditions. One would therefore expect microbes (phytoplankton and bacteria/yeast) and (annual and perennial) plants to be driven by distinct processes, unlike what we report on here. Our results, therefore, provide evidence that ecological groups with superficially similar ecology can be driven by different processes and sustain different levels of biodiversity.

The processes we quantified are the net result of multiple underlying mechanisms leading to multiple kinds of species interactions. Thus, the detection of specific interaction types (e.g. positive ones, Adler, Smull, et al. (2018) and Picoche and Barraquand (2020)) in a community does not guarantee specific processes (e.g. facilitation) will emerge in that community. A corollary of this is that our analysis gives no information about the prevalence of, for example, positive, asymmetric, or correlated species interactions – it only reflects the net result of such interactions. Thus, findings that positive interactions can be abundant in nature (Choler et al., 2001; Martorell and Freckleton, 2014; Soliveres et al., 2015; Wainwright et al., 2016; Bimler et al., 2018; Adler, Smull, et al., 2018; Picoche and Barraquand, 2020) do not contradict our result that net facilitation was only frequently observed in perennial plants and phytoplankton.

Confirming our hypothesis, ecological groups differed in the outcome of species interaction. The fact that the same processes lead to different outcomes in different ecological groups appears counterintuitive at first but stands to reason. That is because detection of negative frequency dependence is not sufficient to assess coexistence (Chesson, 2000a; Adler, HilleRisLambers, and Levine, 2007). Similarly, while the low prevalence of positive frequency dependence leads to priority effects being rare, positive frequency dependence is a necessary but not sufficient condition for priority effects. For priority effect and exclusion, low and high fitness differences relative to niche difference, respectively, are another condition. Coexistence was the most frequent outcome for perennial plants and phytoplankton, whereas competitive exclusion was most prevalent in annual plant and bacteria/yeast communities.

The observed differences between the ecological groups likely indicate actual ecological differences and do not stem from solely technical differences. For example, the results of Adler, Smull, et al., 2018 imply that niche differences will be stronger in field observations than in an experimental setting, and consequentially are more likely to lead to coexistence. However, both annual perennial plants data stem predominantly from field observations. Similarly, both phytoplankton and bacteria/yeast data stem from lab experiments. The differences between these groups can therefore not stem from a methodological difference. Similarly, there is a strong correlation between the ecological group and the community model used.

However, using a different community model or not using any community model does not alter the outcome of competition, the different probabilities in the outcome of competition are therefore also based on ecological differences.

4.3 Limitations and perspectives

We present a cross-community synthesis of the processes driving community composition and the outcome of species interactions. Like any meta-analysis, it comes with several limitations.

First, our results are only valid for the ecological groups represented in the data, and other ecological groups may behave differently than the ones considered here. Even within one community type, there is a large heterogeneity of the predominant processes and predominant outcomes. Hence, refined grouping could be applied. For instance, plants have different life stages associated with specific ecology, potentially leading to different interacting mechanisms captured by diverse global processes. Previous studies have shown that plants at their recruitment stage experience a stronger niche differentiation (Adler, Ellner, et al., 2010; Chu and Adler, 2015; Hallett, Shoemaker, et al., 2019). A clear separation between life stages has the potential to state if this pattern is common among plants and generalize beyond plant. Separation based on a specific ecological characteristic, such as the pigment composition in phytoplankton, could also be interesting to

highlight the importance of evolutive convergence/divergence, here in resource uptake, for coexistence (Stomp et al., 2004; Spaak and De Laender, 2021). Thus, more complex grouping could be applied to our data set to investigate a wide range of ecological questions.

Second, we have little mechanistic understanding of why coexisting species exhibit higher niche differences leading to a prevalence of negative frequency dependence. Various mechanisms can be responsible for this result, including mechanisms driven by specific organismal traits (Gallego et al., 2019; Kraft et al., 2015), phenological traits (Godoy and Levine, 2014; Farrer et al., 2010; Martorell and Freckleton, 2014; Adler, HilleRisLambers, and Levine, 2009) as well as fluctuation-independent (Armitage and Jones, 2019) and fluctuation-dependant mechanisms (Hallett, Shoemaker, et al., 2019). To provide such understanding here would be purely speculative given our diverse data set. Only a general hypothesis can be emitted as niche differences matter across all ecological groups. Our data set contains mostly locally co-occurring species which have connected evolutionary trajectories. That is, the species pairs we analyzed survived assembly through adaptation to their local biotic and abiotic environment. We hypothesized that coexisting species have co-evolved to maximize their niche difference. This hypothesis is aligned with classical thinking (Macarthur and Levins, 1967; Slatkin, 1980; Stomp et al., 2004) and recent work (Zhao et al., 2016), but also challenges

recent findings, suggesting the predominant interaction of evolution with fitness differences rather than niche differences (Hart et al., 2019; Germain et al., 2020; Pastore et al., 2021) Hence, the role of evolution in driving ecological outcomes needs to be evaluated in further detail.

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Figures

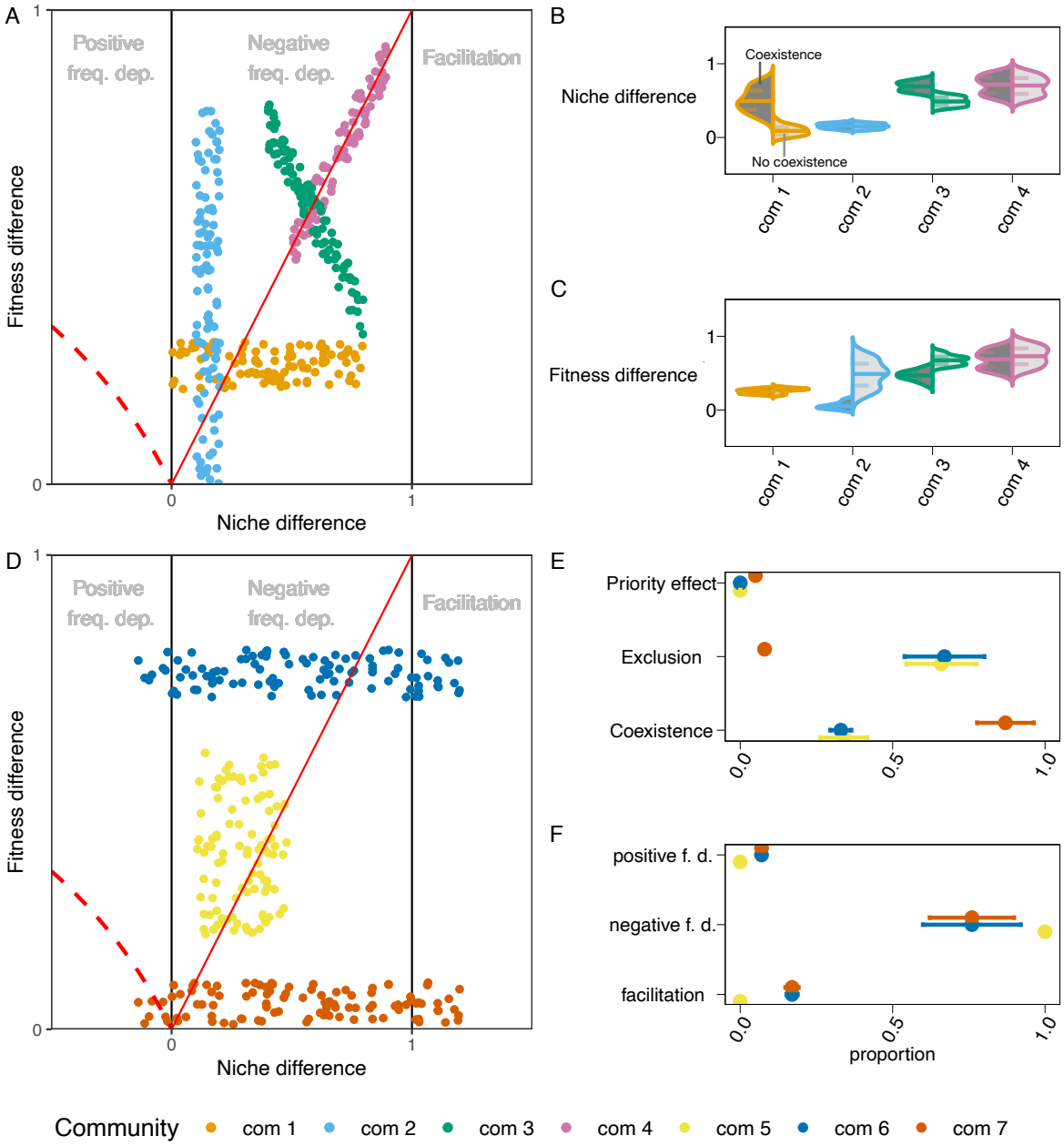

Figure 1: A: Hypothetical distribution of niche and fitness differences for four different community types. Each dot represents niche and fitness difference of the inferior competitor from a two-species community. We assume that communities with higher niche than fitness differences will coexist (below red line). B,C: The four community types differ in whether coexisting communities will have larger niche differences on average (community 1 and 2) and/or smaller fitness differences on average(community 2 and 3). D: Similar to A. Niche differences give insight into the process driving the community (positive frequency dependence +fd, negative frequency dependence -fd and facilitation). Together with fitness differences we can asses the competitive outcome (priority effects, exclusion or coexistence). E,F: The community 5 and 6 do not differ in their proportion for the competitive outcomes, however, they are driven by different processes. Conversely, the community 6 and 7 are driven by the same processes, but they have different proportions of competitive outcomes.

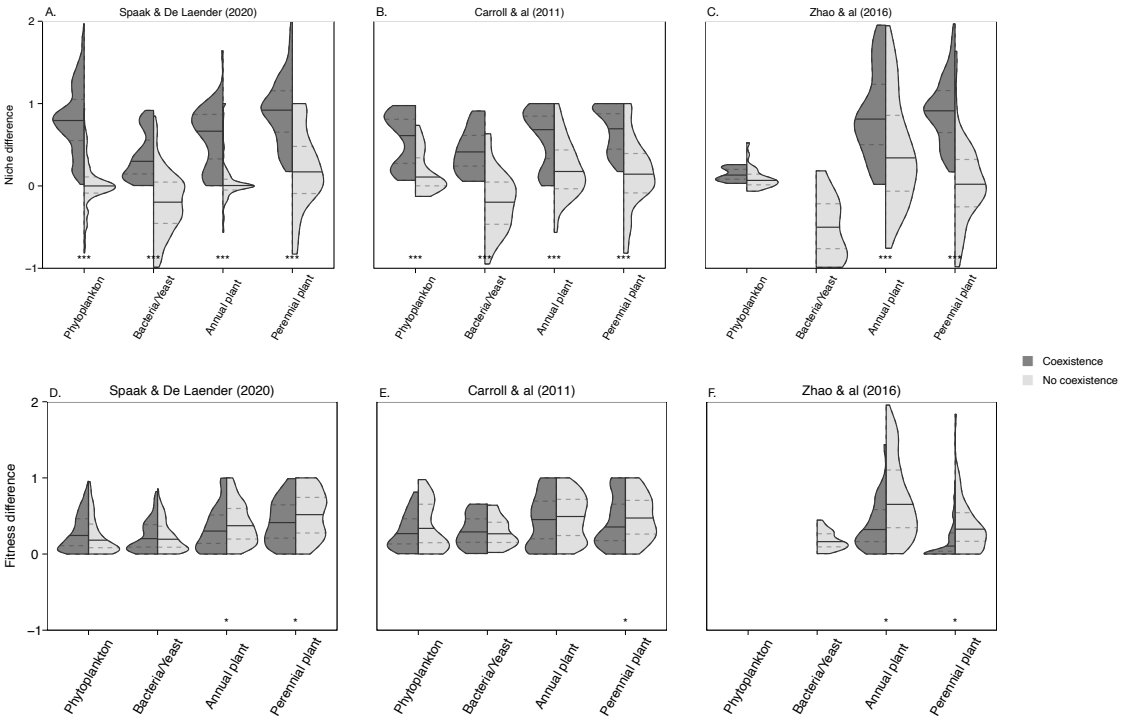

Figure 2: Niche difference is consistently identified as the driver of coexistence. All community types have higher $\mathcal{N}$ for their coexisting communities except for phytoplankton according to Zhao et al. (2016)'s definition. The difference in $\mathcal{F}$ between coexisting and non-coexisting communities is often not significant, except for perennial plant communities. Additionally, the differences are comparatively small. Therefore, the distribution of niche and fitness differences resemble conceptually the distribution of the orange community type from figure 1 A. The median is indicated by the full line and the dashed lines indicate the 25 and 75 quartiles of the distribution. The stars show the significant of the Kolmogorov-Smirnov Test between the distributions of coexisting communities and non-coexisting communities: * = pvalue < 0.05; ** = pvalue < 0.01; *** = pvalue < 0.001. Similar to figure 1 B and C.

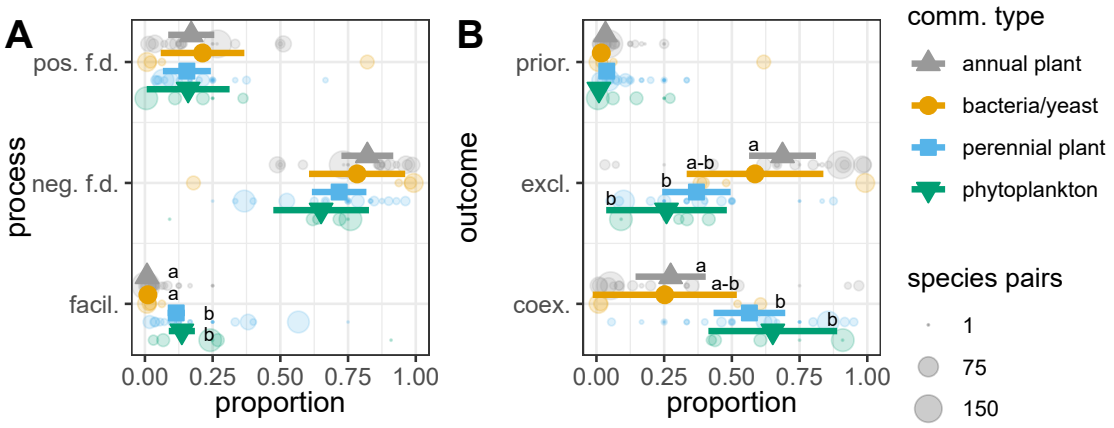

Figure 3: A: The different community types did not differ much in their proportion of the different processes. Negative frequency was the most prevalent in all communities and the proportion of communities driven by negative frequency dependence does not differ significantly between community types. Similarly, the proportion of communities driven by positive frequency dependence did not differ significantly between community types. The proportion differed only for facilitation, where we observed close to no facilitation for annual plants and bacteria/yeast communities (labelled as "a"), in contrast to perennial plants or phytoplankton (labelled as "b"). B: Some of the different community types did differ in their proportion of the outcomes. For annual plants (labelled as "a") and bacteria/yeast communities (labelled as "a–b"), competitive exclusion was most prevalent, while for coexistence was most prevalent for perennial plants and phytoplankton (labelled as "b"). Priority effects were rare in all community types. The distributions of niche and fitness differences for bacteria/yeast and annual plant communities therefore resemble most the community 6 from figure 1 D. Perennial plant and phytoplankton communities resemble most the community 7.The different prevalence of the different processes and outcomes, and the similarity of this prevalence across community types, was confirmed by the estimated factors associated to the community types of the fitted linear mixed-effects models of the meta-analyses, and on the heterogeneity explained with the community type (table S7). A,B: Marker and bar show the mean and confidence interval. The dots indicate the proportion for each individual study, whereas the weight (number of communities per study) is shown by its size. Distributions with same labels do not differ significantly. Distribution with two labels ("a–b"), indicate that do not differ significantly with the distributions of either of the labels.Similar to figure 1 E and F.

6 Appendix

6.1 Collection of data

	Definition	Initial paper include data	Number of paper citing the definition until the 14th of December 2020	Refined if number of paper >100	Empirical papers including the computation of ND and FD
	Godoy, Kraft, et al. (2014)	1	96	96	23
	Carroll et al. (2011)	0	104	43	18
	Adler, HilleRis-Lambers, et al. (2007)	0	639	83	11
	Chesson (1990b)	0	3327	204	15
	Spaak and De Laender (2020)	1	2	2	0
	Zhao et al. (2016)	1	6	6	0
	Bimler et al. (2018)	1	20	20	6
	Saavedra et al. (2017)	0	58	58	5
	Chesson (2003)	0	83	83	6
	Chesson and Kuang (2008)	0	251	23	6
	Carmel et al. (2017)	0	10	10	1
number total of papers:	11	4	4596	628	91
with the initial paper included:			4607	639	95
minus duplicate papers:					50
minus duplicate databases or non-available databases:			38		29

Table S1: The searching and refining processes lead us to use the data of 29 papers.

	Field	Mesocosm	Greenhouse	lab	Total
Phytoplankton	0.0	0.0	0.0	184.0	184.0
Bacteria	0	0	0	728	728.0
Annual plant	396	39	6	28	469.0
Perennial plant	215	0	18	28	261.0

Table S2: For each ecological group we report how many communities stem from which experimental setting. Phytoplankton and Bacteria have exclusively been analysed in laboratory settings. Similarly, annual and perennial plants have predominantly been analysed in a field setting. However, the differences in their competitive outcomes are unlikely to stem from these differences, as phytoplankton differ from bacterial communities, while both have been analysed in lab environments. Similarly, annual and perennial plants differ in their competitive outcomes, yet both data-sets stem predominantly from field data.

	Lotka Volterra	APM	AP2	None	Total
Phytoplankton	0.0	0.0	0.0	184.0	184.0
Bacteria	0	0	0	728	728.0
Annual plant	34	412	12	11	469.0
Perennial plant	253	8	0	0	261.0

Table S3: For each ecological group we report how many communities stem have been fitted with which community model. Phytoplankton and Bacteria have exclusively been analysed without a community model. Annual plants have predominantly been analysed with the Beverton-Holt annual plant model while perennial plants have predominantly been analysed with the Lotka-Volterra community model.

Paper	Community type	Definition of ND and FD used	Population model used	Field or lab experiment	Number of 2 species communities
Bimler et al. (2018)	Annual plant	Bimler et al. (2018)	AP2	field	12
Godoy and Levine (2014)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	153
Godoy, Kraft, et al. (2014)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	15
Germain et al. (2016)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	36
Rey et al. (2017)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	2

Hallett et al. (2018)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	15
Lanuza et al. (2018)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	15
Matias et al. (2018)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	45
Petry et al. (2018)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	55
Wainwright et al. (2019)	Annual plant	Godoy, Kraft, et al. (2014)	APM	field	24
Siefert et al. (2019)	Annual plant	Adler	APM	lab	12

Blackford et al. (2020)	Annual plant	Godoy, Kraft, et al. (2014)	APM	lab	1
Armitage and Jones (2019)	Annual plant	Chesson (1990b)	Lotka Volterra	lab	1
Ke and Letten (2018)	Annual plant	Chesson (1990b)	Lotka Volterra	lab	3
Ocampo-Ariza et al. (2018)	Annual plant	Carroll et al. (2011)	None	lab	1
Zhang and Kleunen (2019)	Annual plant	Saavedra	APM	mesocosm	39
Tan et al. (2016)	Bacteria/Yeast	Carroll et al. (2011)	None	lab	7
Grainger et al. (2019)	Bacteria/Yeast	Carroll et al. (2011)	None	lab	32

Li Shao-peng et al. (2019)	Bacteria/Yeast	Carroll et al. (2011)	None	lab	24
Zhao et al. (2016)	Bacteria/Yeast	Zhao	None	lab	65
Cardinaux et al. (2018)	Perennial plant	Godoy	APM	field	8
Veresoglou et al. (2018)	Perennial plant	Chesson (1990b)	Lotka Volterra	lab	28
Adler, Smull, et al. (2018)	Perennial plant	Chesson (1990b)	Lotka Volterra	NA	255
Narwani et al. (2013)	Phytoplankton	Carroll et al. (2011)	None	lab	27
Venail et al. (2014)	Phytoplankton	Carroll et al. (2011)	None	lab	27
Gallego et al. (2019)	Phytoplankton	Carroll et al. (2011)	None	lab	15

Jackrel et al. (2020)	Phytoplankton	Carroll et al. (2011)	None	lab	99
Jia et al. (2020)	Phytoplankton	Carroll et al. (2011)	None	lab	1
Spaak and De Laender (2020)	Phytoplankton	Spaak and De Laender (2020)	None	lab	1
Total	29				1018

Table S4: Details of the 29 papers providing the data set used for the meta-analysis. Note that Adler, Smull, et al. (2018) is a meta-analysis gathering multiple papers. APM = Annual plant model; AP2 = Second annual plant model, that is the logarithm form of APM Bimler et al. (2018)

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6.2 Computation of three model-independent definitions

We denote the monoculture growth rate as μ_i, the invasion growth rate as r_i, the no-niche growth rate η_i and the monoculture equilibrium density as N_i^*. With this we can define the three model independent definitions. For Spaak and De Laender, 2020 we define

$$\mathcal{N}_i = \frac{r_i - \eta_i}{\mu_i - \eta_i} \tag{S1}$$

$$\mathcal{F}_i = \frac{\eta_i}{\mu_i - \eta_i} \tag{S2}$$

For Carroll et al., 2011 we define

$$\mathcal{N}_i = \mathcal{N}_| = 1 - \sqrt{\frac{\mu_i - r_i}{\mu_i} \cdot \frac{\mu_j - r_j}{\mu_j}} \tag{S3}$$

$$\mathcal{F}_i = \sqrt{\frac{\mu_i - r_i}{\mu_i} \cdot \frac{\mu_j}{\mu_j - r_j}} \tag{S4}$$

And for Zhao et al., 2016 we define

$$\mathcal{N}_i = \mathcal{N}_j = \frac{r_i + r_j}{2}\mathcal{F}_i = \log_{10}\left(\frac{N_i^*}{N_j^*}\right) \tag{S5}$$

We adjusted the definitions of Carroll et al., 2011 and Zhao et al., 2016 slightly

to facilitate inter-definition comparisons. These adjustments are purely aesthetic and do not change the underlying concepts. We changed the definitions such that a neutral community will have $\mathcal{N} = \mathcal{F} = 0$ and that a species persists if $\mathcal{N} > \mathcal{F}$ (only for the definition of Carroll et al., 2011).

The necessary parameters μ_i, r_i, η_i and N_i^* where either reported in the original studies or the original papers reported enough information that allowed us to compute these parameters, most notably by reporting the per-capita growth rate function f_i. For time discrete per-capita growth rates functions (e.g. the annual plant model) we first log-transformed the growth rate, i.e. $\hat{f}_i(N_i, N_j) = \log(g_i(N_i, N_j))$.Given the per-capita growth rate function we can compute the monoculture growth rate as $\mu_i = f_i(0, 0)$, the monoculture equilibrium density as the solution of the equation $f_i(N_i^*, 0) = 0$ and the invasion growth rate as $r_i = f_i(0, N_j^*)$.

The only parameter that's left is the no-niche growth rate η_i, which is defined in Spaak and De Laender, 2020. Numerically computing the no-niche growth rate η_i is simple when using automated software (`https://github.com/juergspaak/NFD_definitions`). To do so, one has to solve the following two equations

$$c_i \cdot c_j = 1 \tag{S6}$$

$$\left| \frac{\mu_i - r_i}{\mu_i - f_i(c_j N_j^*, 0)} \right| = \left| \frac{\mu_j - r_j}{\mu_j - f_j(c_i N_i^*, 0)} \right| \tag{S7}$$

$\mu_i, \mu_j, r_i, r_j, N_i^*$ and N_j^* can be computed before hand and can therefore be treated as constants in this equation. The only two variables are c_i and c_j, whereof one can easily be eliminated with equation S6. Essentially, one therefore has to solve a one-dimensional equation. This equation might not be solvable by hand, but can easily be solved by numerical means. Importantly, if both species are strictly negative density dependence in monocultures, which is the case for most applications of modern coexistence theory, then the equation to solve is monotonic in c_i or c_j as well, which further simplifies numerical solutions.

Rather, the challenging part is to biologically justify the equations S6 and S7. c_i converts density of species i to densities of species j, and similarly c_j converts densities of species j to densities of species i. Consequently, $c_i \cdot c_j$ converts densities of species i to densities of species i and must therefore be one, which explains equation S6.

The c are chosen such that they conserve total density, same total density implies same total effect on growth rates. $1 - \frac{r_i}{\mu_i}$ can be interpreted as the relative

effect species j has on the growth rate of species i. Similarly, $1 - \frac{\eta_j}{\mu_j}$ denotes the relative effect species j has on itself. The total effect of species j is therefore $\left(1 - \frac{r_i}{\mu_i}\right)\left(1 - \frac{\eta_j}{\mu_j}\right)$, which must be equal to the total effect of species i, which is $\left(1 - \frac{r_j}{\mu_j}\right)\left(1 - \frac{\eta_i}{\mu_i}\right)$. By reordering we obtain equation S7.

For the cases where the no-niche growth rate was not measured and could not be computed given the literature data we were able to approximate the definition of Spaak and De Laender, 2020 given the invasion and intrinsic growth rates μ_i. First we note that for exactly one species η_i is positive.

$$\eta_i = f_i(c_j N_j^*, 0) > 0 = f_i(N_i^*, 0) \tag{S8}$$

$$\Leftrightarrow c_j N_j^* < N_i^* \tag{S9}$$

$$\Leftrightarrow N_j^* < \frac{N_i^*}{c_j} = c_i N_i^* \tag{S10}$$

$$\Leftrightarrow \eta_j = f_j(c_i N_i^*, 0) < 0 = f_j(N_j^*, 0) \tag{S11}$$

Next we observe that

$$\eta_i < 0 \tag{S12}$$

$$\Leftrightarrow \mu_i - \eta_i > \mu_i \tag{S13}$$

$$\Leftrightarrow \frac{1}{\mu_i - \eta_i} < \frac{1}{\mu_i} \tag{S14}$$

$$\Leftrightarrow \frac{|\mu_i - r_i|}{\mu_i - \eta_i} < \frac{|\mu_i - r_i|}{\mu_i} \tag{S15}$$

We now assume, without loss of generality $\eta_i < 0$, which leads to

$$\frac{|\mu_i - r_i|}{\mu_i} > \frac{|\mu_i - r_i|}{\mu_i - \eta_i} = \frac{|\mu_j - r_j|}{\mu_j - \eta_j} > \frac{|\mu_j - r_j|}{\mu_j} \tag{S16}$$

Which is equivalent to

$$\frac{|\mu_i - r_i|}{\mu_i} > \frac{|\mu_i - r_i|}{\mu_i - \eta_i} > \frac{|\mu_j - r_j|}{\mu_j} \tag{S17}$$

$$\frac{\mu_i}{|\mu_i - r_i|} < \frac{\mu_i - \eta_i}{|\mu_i - r_i|} < \frac{\mu_j}{|\mu_j - r_j|} \tag{S18}$$

$$\mu_i < \mu_i - \eta_i < \frac{\mu_j}{|\mu_j - r_j|} \cdot (\mu_i - r_i) \tag{S19}$$

$$0 < -\eta_i < \frac{\mu_j}{|\mu_j - r_j|} \cdot |\mu_i - r_i| - \mu_i \tag{S20}$$

$$0 > \eta_i > \mu_i - \mu_j \frac{|\mu_i - r_i|}{|\mu_j - r_j|} \tag{S21}$$

$$\tag{S22}$$

We therefore chose 10 linearly spaced values for η_i in the interval $[0, \mu_i - \mu_j \left|\frac{\mu_i - r_i}{\mu_j - r_j}\right|]$ and computed $\mathcal{N}_i$ and $\mathcal{F}_i$ based on these values.

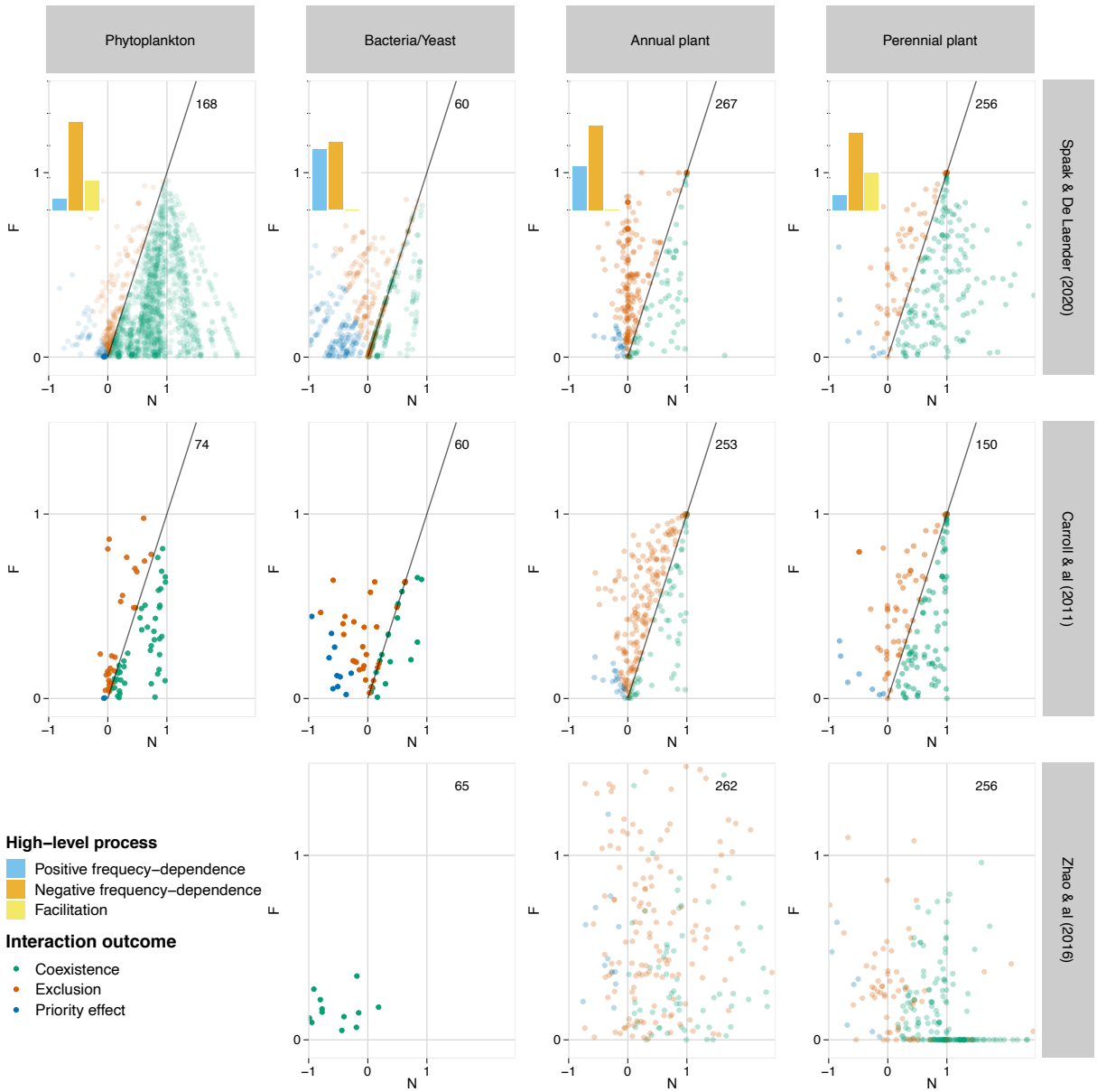

Figure S1: $\mathcal{N}$ and $\mathcal{F}$ for each community split according to community type (columns) and definitions (rows). The different systems include different high level process and ratio of interaction outcome. The definitions associated different potential of ecological interpretation. Spaak and De Laender (2020)'s and Carroll et al. (2011)'s definitions mainly differ in the incorporation of facilitation. However, they both largely differ from Zhao et al. (2016)'s, who tends to have wider spread distributions. It is important to note that the showed $\mathcal{F}$ corresponds to the $\mathcal{F}$ of the inferior species, therefore $\mathcal{F}$ is always bigger than 0. Coexisting communities are green, communities under respectively priority effect and competitive exclusion are blue and red. The transparency is based on the quantity of communities per graph to ensure the same amount of colour per graph. The number of communities is indicated for each graph.

Table S5: The 11 definitions, their frameworks and their restrictions. The symbols correspond to: α_{ij} interaction coefficients, according to Lotka-Volterra model; a_{ij} interaction coefficients, according to the Annual plant model (Chesson, 1990a) ; λ_i per-germinant fecundity in the absence of competition according to the Annual plant model ; K_i environmental carrying capacity of species i; k_{A1} is the per capita rate at which species A consumes resource 1.

Paper	Assumption	mathematical definition	Experimental requirements
Chesson and Kuang (2008)	Mac-Arthur model with predator extension	$\mathcal{N} = 1 - \frac{\sqrt{\alpha^R_{ij}\alpha^R_{ji}}+\sqrt{\alpha^R_{ij}\alpha^R_{ji}}}{s_i s_j}$ $\mathcal{F}_i = \frac{s_j}{s_i}\frac{\mu^R_i-\mu^P_i-m_i}{\mu^R_j-\mu^P_j-m_j}$	Model fitting
Chesson (1990b)	LV-model	$\mathcal{N} = 1 - \sqrt{\frac{a_{ij}a_{ji}}{a_{ii}a_{jj}}}$ $\mathcal{F}_i = \sqrt{\frac{a_{ji}a_{jj}}{a_{ij}a_{ii}}}$	Model fitting

Adler, HilleRis-Lambers, et al. (2007)	Annual plant model	$\mathcal{N}_i = \log\left(\frac{\lambda_j}{1+\frac{a_{ij}}{a_{jj}}(\lambda_j-1)}\right)$ $\mathcal{F}_i = \log(\frac{\lambda_i}{\lambda_j})$	Model fitting
Godoy, Kraft, et al. (2014)	Annual plant model	$\mathcal{N} = 1 - \sqrt{\frac{a_{ij}a_{ji}}{a_{ii}a_{jj}}}$ $\mathcal{F}_i = \frac{\eta_j-1}{\eta_i-1}\sqrt{\frac{a_{ji}a_{jj}}{a_{ij}a_{ii}}}$	Model fitting
Bimler et al. (2018)	Exponential Annual plant model	$\mathcal{N} = 1 - \sqrt{\frac{\exp a_{ij}+a_{ji}}{\exp a_{ii}+a_{jj}}}$ $\mathcal{F}_i = \sqrt{\frac{\exp a_{ji}+a_{jj}}{\exp a_{ij}+a_{ii}}}$	Model fitting
Saavedra et al. (2017)	Linear species interactions	$\mathcal{N} = \frac{2}{\pi}\left(\arcsin \frac{\alpha_{ii}\alpha_{jj}-\alpha_{ij}\alpha_{ji}}{\sqrt{\alpha_{ii}2+\alpha_{ji}2}\sqrt{\alpha_{jj}2+\alpha_{ij}2}}\right)$ $\mathcal{F} = \frac{180}{\pi}\left(\arccos \frac{r.r_c}{\lVert r\rVert.\lVert r_c\rVert}\right)$	Model fitting
Chesson (2003)	Invasion analysis possible, Community model available	$\mathcal{N} = \overline{\frac{\Delta I-\Delta N}{d}}$ $\mathcal{F}_i = \frac{r_i}{d_i} - \mathcal{N}$	Model fitting

Carmel et al. (2017)	Invasion analysis possible, Minimal growth rate is equal to mortality	$\mathcal{N} = 1 - min(\frac{k_{A1}/k_{A2}}{k_{B1}/k_{B2}}, \frac{k_{B1}/k_{B2}}{k_{A1}/k_{A2}})$ $\mathcal{F}_i = min(\frac{k_{A1}k_{A2}}{k_{B1}k_{B2}}, \frac{k_{B1}k_{B2}}{k_{A1}k_{A2}})$	Invasion growth rate, Mortality rate
Zhao et al. (2016)	Invasion analysis possible	$\mathcal{N} = 1 + r_i + r_j$ $\mathcal{F}_i = \log_{10}\left(\frac{K_i}{K_j}\right)$	Invasion growth rate, Equilibrium abundances
Carroll et al. (2011)	Invasion analysis possible	$\mathcal{N} = 1 - \prod_{i=1}^{n} S_i^{1/n}$ $\mathcal{F} = exp\left[\left(\overline{(lnS)^2} - \overline{lnS^2}\right)^{1/2}\right]$	Invasion growth rate, Monoculture growth rate

Spaak and De Laender (2020)	Invasion analysis possible	$\mathcal{N} = \frac{f_i(0,N_j^*)-f_i(c_jN_j^*,0)}{f_i(0,0)-f_i(c_jN_j^*,0)}$ $\mathcal{F}_i = \frac{f_i(c_jN_j^*,0)}{f_i(0,0)} - \frac{f_i(N_j^*,0)}{f_j(0,0)}$	Density over time in mono-culture, Invasion growth rate

Table S6: Conditional probability of the outcome, given the process and the community type, computed from the niche and fitness of all species pairs that appear on the selected studies (Table S4).

Community Type	Process	P(Outcome|Proc.,Comm. Type) (%)		
		Coexistence	Exclusion	Priority
phytoplankton	Negative f. d.	64.4	35.6	0
	Positive f. d.	0	38.3	61.7
	Facilitation	100	0	0
bacteria/yeast	Negative f. d.	71.4	28.6	0
	Positive f. d.	NaN	NaN	NaN
	Facilitation	NaN	NaN	NaN
annual plant	Negative f. d.	41.3	58.7	0
	Positive f. d.	0	75.4	24.6
	Facilitation	100	0	0
perennial plant	Negative f. d.	68.0	32.0	0
	Positive f. d.	0	51.9	48.1
	Facilitation	100	0	0

6.3 Data analysis: odds ratios

Our data represents a three-level contingency table, containing the number of times each combination of community type, process, and outcome was found. In order to analyze differences among ecological groups, we can also compute odds ratios for the different processes and outcomes.

Let $P\,(\text{proc}|i)$ be the probability of a given process for the community type i. This probability can be computed from our data as

$$P\,(\text{proc}|i) = \frac{n_{\text{proc},i}}{\sum_{\text{proc}} n_{\text{proc},i}}\,,$$

where $n_{\text{proc},i}$ is the number of times that a community type i that has been observed with a process "proc". (An analogous expression can be obtained fo the probability of a given outcome for the community type i). From this probability, we can compute the odds of that process for this community type as

$$\mathcal{O}\,(\text{proc}|i) = \frac{P\,(\text{proc}|i)}{1 - P\,(\text{proc}|i)} = \frac{n_{\text{proc},i}}{\sum_{\text{proc}'\neq\text{proc}} n_{\text{proc}',i}}\,. \tag{S23}$$

These odds represent how likely it is to observe that process for the given community type i, compared to any other process. For example, if the odds were 2, we would see this process twice as often as all other processes combined.

With the definition of the odds, we compute the odds ratio (Bland and Altman, 2000) of such process for different ecological groups as

$$\mathcal{OR}\left(\text{proc}|j,i\right) = \frac{P\left(\text{proc}|j\right)/\left(1-P\left(\text{proc}|j\right)\right)}{P\left(\text{proc}|i\right)/\left(1-P\left(\text{proc}|i\right)\right)} \tag{S24}$$

Such odds ratio compare the odds of observing the desired process between ecological groups i and j. If $\mathcal{OR} = 1$, the odds of observing this process for the community i equals the odds of finding it in community j. If $\mathcal{OR} > 1$ ($\mathcal{OR} < 1$), the process would occur more (less) frequently for community type j than for community type i.

In order to compute the confidence intervals of the obtained odds ratios, we must consider two different contributions.

On the one hand, in some situations was not possible to obtain from the studies the no-niche growth rates, as we mentionned on the previous section. For these cases, we took 10 linearly spaced values for η_i and computed niche and fitness differences based on these values. This causes a variation on $\mathcal{N}_i$ and $\mathcal{F}_i$, that might cause a certain variation on the proportion of the outcomes and processes, and hence on the computed odds ratios. we denote $\left(\sigma_\eta\left[\log\mathcal{OR}\left(\text{proc}|j,i\right)\right]\right)^2$ the variance on the computed log odds ratios of the process for a given pair of ecological groups.

Secondly, the finite size of the data will cause that the estimated odds ratios might

differ from the actual values. This implies that there exists a certain uncertainty on the estimated ratios. To compute such uncertainty associated with the finite size of our data, we accounted for the fact that the sampled odd ratios are approximately log-normally distributed. The standard error of the log-transformed odds ratio is given by the sum of reciprocals of the frequencies (Morris and Gardner, 1988)

$$SE_{size}\left[\log \mathcal{OR}\left(\text{proc}|j,i\right)\right] = \sqrt{\frac{1}{n_{\text{proc},i}} + \frac{1}{\sum_{\text{proc}'\neq\text{proc}} n_{\text{proc}',i}} + \frac{1}{n_{\text{proc},j}} + \frac{1}{\sum_{\text{proc}'\neq\text{proc}} n_{\text{proc}',j}}}\,. \tag{S25}$$

Putting together these two contributions, the total standard error of the estimated odds ratios would simply be

$$SE_{total} = \sqrt{\sigma_\eta^2 + SE_{size}^2}\,. \tag{S26}$$

Hence, the 95% confidence level interval for the odds ratios between the two communities would be

$$\mathcal{OR} \times \exp\left\{\pm 1.96\ SE_{total}\left[\log \mathcal{OR}\right]\right\}\,. \tag{S27}$$

If the 95% confidence interval of the odds ratios contained 1, we concluded that the process is equally likely in both ecological groups. Conversely, if this was not the case, we concluded that the process was not equally likely in both ecological

groups. We applied an identical procedure to test for among-community differences in the occurrence of the various outcomes.

In Figs. S2 and S3, we can observe the computed odds ratios for the different possible processes and outcomes for the different ecological groups. With respect to the processes (Fig. S2), both annual plants and bacteria/yeast were now more often driven by positive or negative frequency dependence than the other ecological groups, although the differences are small.Facilitation was now more probable for perennial plants or phytoplankton. With respect to the outcomes (Fig. S3), the competitive exclusion was now more common for annual plants and bacteria/yeast than for perennial plants or phytoplankton; the opposite occurred for coexistence. The main difference between this "odd-ratio" method and the meta-analysis is that the former more often suggested the obtained relations to be significant (Fig. **??**).

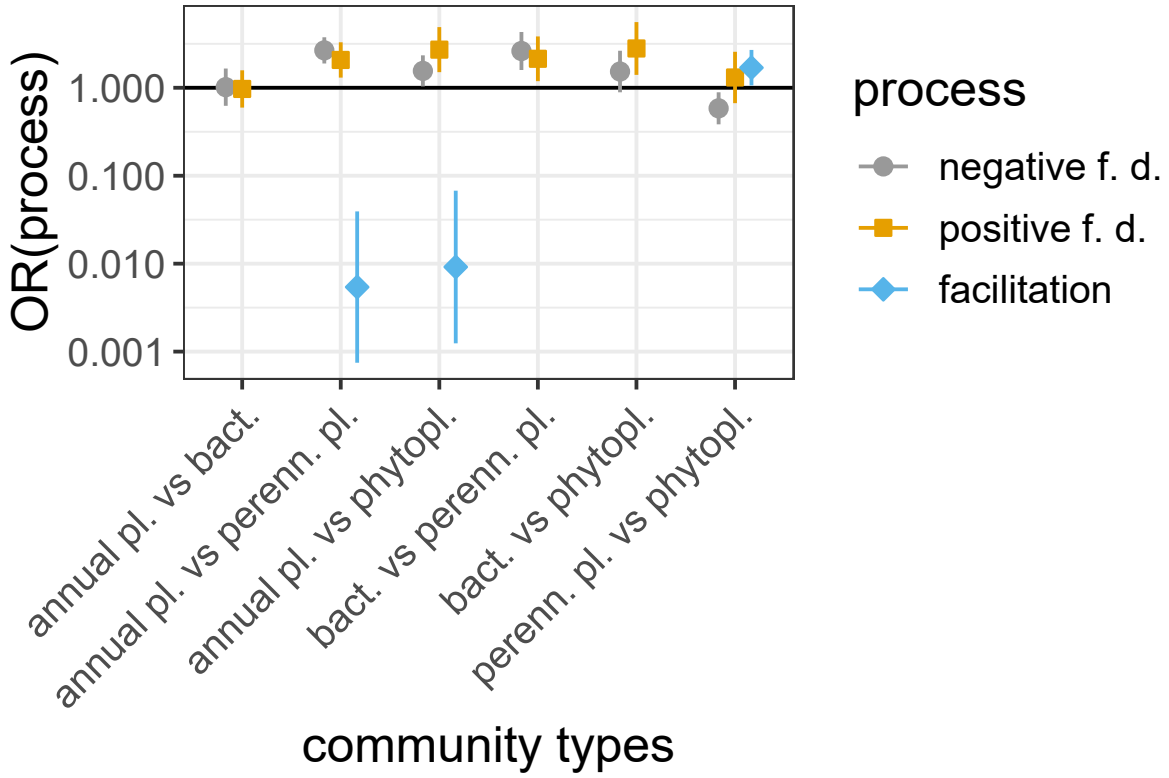

Figure S2: Odds ratios in favor of a given process (negative frequency dependence, positive frequency dependence, or facilitation) if the species belong to the community type 1 versus if the species belong to the community type 2. The error bars corresponds to the 95% confidence intervals.

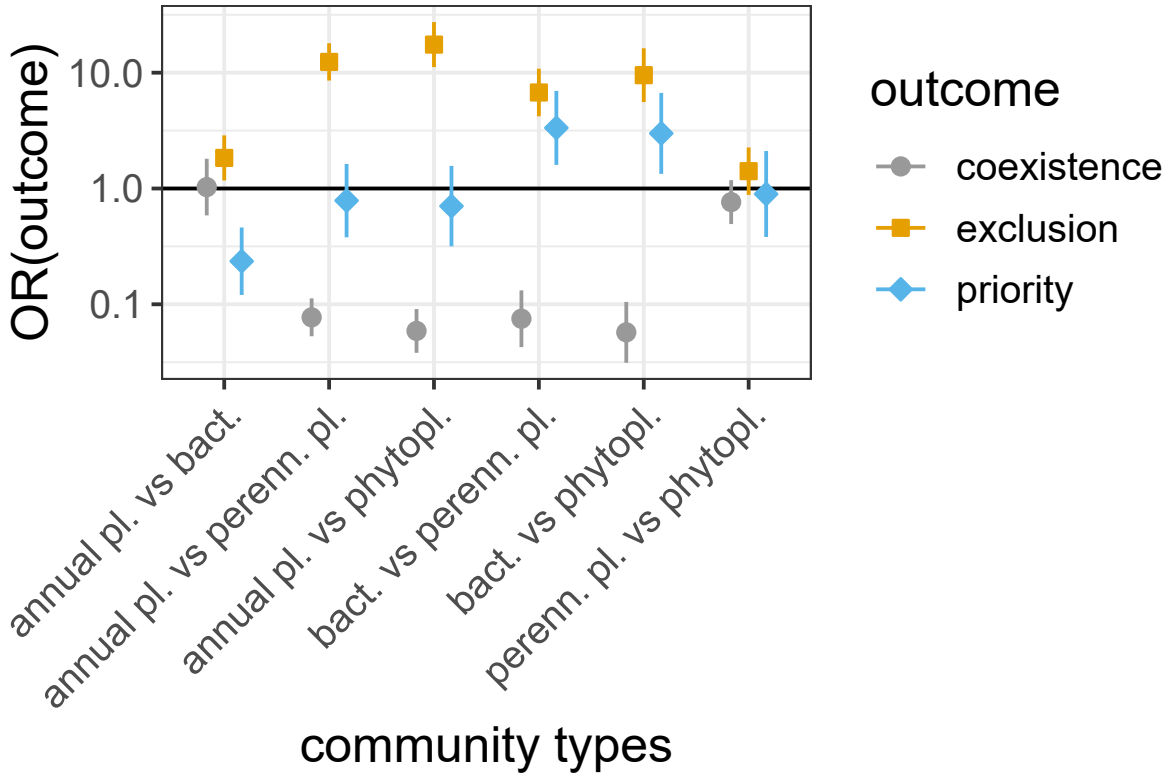

Figure S3: Odds ratio in favor of a given outcome (coexistence, competitive exclusion, or priority effect) if the species belong to the community type 1 versus if the species belongs to the community type 2. The error bars corresponds to the 95% confidence intervals.

6.4 Data meta-analysis

Proportion of the different processes

	Positive F. D.	Negative F. D.	Facilitation
k	52	52	52
R^2	1.93%	8.97%	99.94%
QM/QE	0/273	4/340	65/150
Intercept	**0.171 ± 0.085 *****	**0.821 ± 0.096 *****	0.0077 ± 0.0084 ·
CT:bact~a.p.	0.04 ± 0.18	−0.04 ± 0.20	0.00 ± 0.12
CT:p.p~a.p.	−0.02 ± 0.12	−0.10 ± 0.14	**0.108 ± 0.033 *****
CT:phyto~a.p.	−0.01 ± 0.18	−0.17 ± 0.20	**0.129 ± 0.049 *****

Proportion of the different outcomes

	Coexistence	Exclusion	Priority
k	52	52	52
R^2	26.82%	30.67%	100%
QM/QE	15/800	18/750	7/85
Intercept	**0.27 ± 0.13 *****	**0.69 ± 0.12 *****	**0.033 ± 0.016 *****
CT:bact~a.p.	−0.02 ± 0.30	−0.10 ± 0.28	0.015 ± 0.025
CT:p.p~a.p.	**0.29 ± 0.19 ****	**−0.32 ± 0.18 *****	0.005 ± 0.028
CT:phyto~a.p.	**0.38 ± 0.27 ****	**−0.43 ± 0.25 *****	**−0.024 ± 0.021 ***

Table S7: Results of weighted mixed-effect meta-analysis for the proportion of the different processes (upper panel) and outcome (lower panel). For each analysis we give the number of studies (k), an estimate of the explained variance (R^2), the model and error heterogeneity (QM, QE) and then parameter estimates for the intercept and contrasts for each community type [annual plant (a.p.) vs bacteria/yeast (bact), perennial plant (p.p.) and phytoplankton (phyto), respectively]. The proportion of the processes positive frequency dependence or negative frequency dependence do not differ for the different ecological groups (since the estimators associated with the community type factors are not significantly different from zero, and their p-values are higher than 10^{-1}); however, the proportion of facilitation is significantly higher for perennial plants and phytplankton than for annual plants or bacteria/yeast (significant positive estimators associated with these facotrs, with p-values smaller than 10^{-3}). With respect to proportion of outcomes, coexistence is significatively more frequent in perennial plants and phytoplankton than in annual plants; exclussion is less frequent for the former ecological groups than for annual plants; and the proportion of facilitations is slightly less frequent for phytoplankton than for annual plants. $***$ denotes that the estimated moderator has a significance of $p \leq 10^{-3}$; $**$ denotes that $10^{-3} < p \leq 10^{-2}$; $*$ denote that the value present a significance of $10^{-2} < p \leq 5 \cdot 10^{-2}$; and $\cdot$ represents a slightly significant value, with $5 \cdot 10^{-2} < p \leq 10^{-1}$.

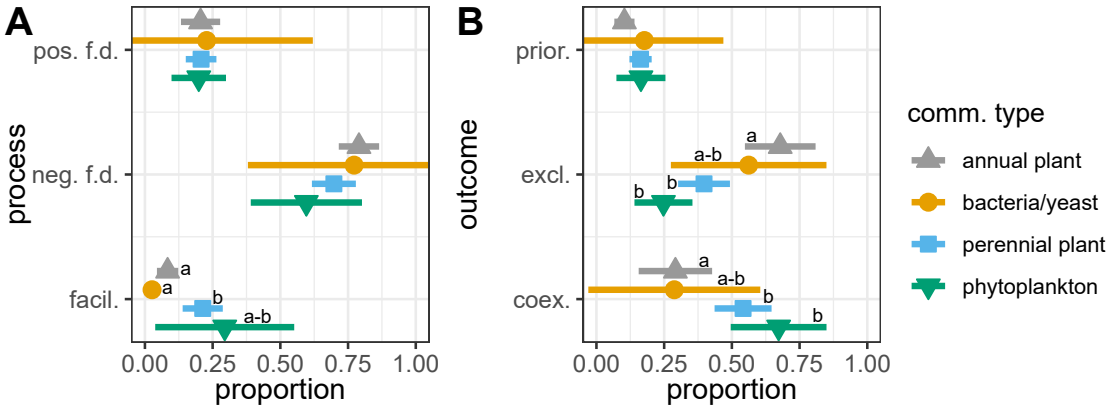

Figure S4: Similar to Fig. 3. In Fig. 3, a proportion is computed for each study (transparent points), with a variance that greatly depends on the number of species pairs analyzed in each study. The average proportion of the different processes and outcomes is computed using these variances as weights. Here, the average proportions across studies are computed as simple arithmetic means, no considering different weights. The results do not differ too much. A: There are no significant differences across communities in the proportions of positive frequency dependence and negative frequency dependence. For facilitation, it seems to hardly occur for annual plants and bacteria/yeast, while it seems more frequent for perennial plants and phytoplankton. B: ecological groups do not significantly differ in the proportion of priority effects outcome. Moreover, for annual plants the proportion of exclusion is significantly higher than for perennial plants and phytoplankton, while the opposite occur for exclusion. The distributions of outcomes of bacteria/yeast do not significantly differ of the distribution of any of the other ecological groups. A,B: Marker and bar show the mean and confidence interval. Distributions with same labels do not differ significantly. Distribution with two labels ("a–b"), indicate that do not differ significantly with the distributions of either of the labels.