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## Niche differences, not fitness differences, explain predicted coexistence across ecological groups

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**1. Background:** Understanding the drivers of species coexistence is essential in ecology. Niche and fitness differences (i.e, how species limit themselves compared to others and species' differences in competitive ability, respectively) permit studying the consequences of species interactions. Yet, the multitude of methods to compute niche and fitness differences hampers cross-community comparisons. Such shortcoming leaves a gap in our understanding of the natural drivers of species coexistence and whether niche or/and fitness differences capture them.

**2. Analysis:** Here, we standardised niche and fitness differences across 953 species pairs to investigate species coexistence across ecological groups and methodological settings (experimental setup, natural co-occurrence, population model used, and growth method). Using data gathered from 29 empirical papers, we asked if large niche differences, small fitness differences, or both, explain predicted coexistence. Moreover, we performed an automated clustering algorithm to understand whether different underlying mechanisms drive species interactions. Finally, we tested whether any ecological or/and methodological settings drive these clusters.

**3. Results:** Species pairs predicted to coexist have larger niche differences but not smaller fitness differences than species pairs predicted not to coexist. Also, species pairs group into two clear clusters along the niche difference axis: those predicted to coexist and those that are not. Surprisingly, ecological or methodological settings do not drive these clusters.

**4. Synthesis:** Overall, our results show that species coexistence is mainly influenced by mechanisms acting on niche differences, highlighting the importance of sustaining mechanisms that promote niche differences to maintain species coexistence. In addition, our results provide evidence that communities predicted to coexist differ from those that are not in ways that transcend their ecological grouping.

## 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 (Barabás *et al.*, 2018; Chesson, 2000b, 2020; Saavedra *et al.*, 2017; Spaak *et al.*, 2021). One challenge is that, even at a local scale, the diversity of potential mechanisms is overwhelming and difficult to track (Pilosof *et al.*, 2017). We lack a synthetic insight into how the diversity of specific mechanisms, observed across various ecological groups, maps on to species coexistence. Achieving such a synthesis is challenging because these mechanisms can differ among ecological groups and are typically analysed with different methods.

One way to overcome this limitation is by applying the concepts of niche and fitness differences across different ecological groups (Chesson, 2000b; Spaak & De Laender, 2020; Spaak *et al.*, 2021; ?). Specifically, niche differences measure how much species limit themselves compared to others, while fitness differences measure how competitive ability (e.g., fecundity rate or success, dispersal range) varies among species pairs (Barabás *et al.*, 2018; Chesson, 2000b). These concepts may then act as a common currency and permit synthesis (Grainger *et al.*, 2019b). While species pairs can physically interact via an unlimited number of mechanisms, information on niche and fitness differences can categorise all these mechanisms into a small number of high-level processes (positive, negative, or no frequency dependence respectively, and facilitation), as well as the expected outcomes of these processes (competitive exclusion, coexistence, and priority effects) (Spaak *et al.*, 2021). Frequency dependence occurs when the population growth rate of a species depends on its relative abundance, with the total abundance of all species kept constant (Adler *et al.*, 2007; Ke & Letten, 2018). When frequency dependence is negative (positive), species grow less well when their relative abundance is high (low). Facilitation occurs when population growth is boosted by the presence of a second species (Bimler *et al.*, 2018; Spaak &

Coexistence| modern coexistence theory| ecological groups| methodological settings| meta-analysis| species interactions| clustering

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De Laender, 2020). Competitive exclusion (coexistence) occurs when species pairs cannot (can) persist together, irrespective of their initial abundance. Priority effects involve exclusion dependent on initial abundance (Ke & Letten, 2018; Mordecai, 2011).

Niche and fitness differences have been applied in the past to synthesise the causes and consequences of species interactions (e.g. Adler *et al.* (2007); Godoy *et al.* (2014); Godoy & Levine (2014); Narwani *et al.* (2013)). However, their use comes with a significant limitation: there is not a generally accepted method on how to measure niche and fitness differences (Godwin *et al.*, 2020; Song *et al.*, 2019). Instead, there are, at present, eleven different methods to assess niche and fitness differences (Koffel *et al.*, 2021; Spaak & De Laender, 2020). Many of these methods are tailored to a specific community model and, consequentially, have only been applied to ecological groups, which these models well describe (Bimler *et al.*, 2018; Godoy, 2019). This specificity has hampered cross-community comparison. Recently, we developed a method to assess niche and fitness differences (Spaak & De Laender, 2020; Spaak *et al.*, 2021), which allows computing niche and fitness differences in a standardised way or converting available data into a common currency. Given this method, it is now possible to use niche and fitness differences as a common currency across multiple ecological groups to ask what permits or hampers species coexistence (Germain *et al.*, 2016; Grainger *et al.*, 2019b; Narwani *et al.*, 2013).

In principle, coexistence can occur when niche differences (promoting coexistence) are large, when fitness differences (hampering coexistence) are small, or when both occur. The importance of the former for coexistence has been demonstrated (mostly in plants) in both semi-natural (Adler *et al.*, 2010, 2018; Armitage & Jones, 2019; Chu & Adler, 2015; Godoy *et al.*, 2017) and experimental communities (Li *et al.*, 2019; Mathias & Chesson, 2013; Narwani *et al.*, 2013). However, small fitness differences have also been found to promote the prediction of coexistence (Chu & Adler, 2015). Thus, it is not clear what drives the prediction of coexistence in natural systems: fitness differences, niche differences, or both. Therefore, the first outstanding question is whether, across multiple ecological groups, large niche difference, small fitness difference, or both explain predicted coexistence.

Next, we might ask whether there is a gradual or abrupt change in how species predicted to coexist or not interact within each other. Specifically, if species pairs predicted to coexist differ from the ones predicted to not coexist only in the relative strength of these underlying species interactions, then we would expect a gradual change of niche and fitness differences from coexistence to competitive exclusion. Conversely, if predicted coexistence is driven, at least partially, by fundamentally different underlying species interactions, then we expect a different distribution of niche or fitness differences for coexist-

ing communities than for non-coexisting communities. For example, neutrally co-occurring species pairs differ conceptually in their underlying species interactions from stably coexisting species (Chesson, 2000a; Hubbell, 2001), which leads to a gap in their distributions of niche and fitness differences (Song *et al.*, 2019). Therefore, a second outstanding question is whether species pairs cluster in the niche differences - fitness differences space. Here, we performed a meta-analysis of species-interaction data on 953 species pairs in four ecological groups (phytoplankton, bacteria/yeast, annual and perennial plants) to understand the drivers of coexistence. While the four ecological groups do not represent the diversity of natural systems, they represent a variety of life spans, reproduction strategies, and habitats. We first quantified niche and fitness differences using one broadly applicable definition (Spaak & De Laender, 2020; Spaak *et al.*, 2021). Then, because species interaction experiments are typically short-term, we predict long-term coexistence from the computed niche and fitness differences (Spaak & De Laender, 2020). Next, we tested the hypothesis that niche differences (noted as  $\mathcal{N}$  or ND) and fitness differences (noted as  $\mathcal{F}$  or FD) were larger and smaller, respectively, in species pairs predicted to coexist, thus jointly promoting coexistence. We found that coexistence is mainly driven by niche and not fitness differences. We then conducted a clustering analysis in niche and fitness differences space to test for generalities across communities. This procedure identified two distinctly segregated clusters (each representing 40% of the data) that were only driven by niche differences and not by ecological group membership or methodological differences. We conclude that, for the four ecological groups considered, species predicted to coexist differ from the ones predicted to not coexist because they have higher niche differences. Additionally, there is broad similarity across the inspected communities, as they can be grouped in mainly two clusters. The sharp boundary between and community diversity within these clusters hints at the existence of unrecorded factors driving niche differences.

## Methods

**Data collection.** We searched the literature for experimental measurements of niche and fitness differences (see Fig. ?? for an overview). To do so, we first identified eleven papers that have introduced a definition of niche and fitness differences (See Appendix, Table ??) and gathered all papers that cited one of these eleven original definitions by the 14<sup>th</sup> of December 2020. For the highly cited definitions, more than 100 citations (Adler *et al.*, 2007; Chesson, 2000b; Chesson & Kuang, 2008), we refined the search with the following keywords: ("niche differences" OR "niche overlap" OR "stabilising mechanisms") AND ("fitness differences" OR "fitness " OR "equaliseing mechanism") AND ("Experiment" OR "Data" OR "Field") AND ("Competition" OR "Coexis-

tence"). Only 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 (Bimler *et al.*, 2018; Carroll *et al.*, 2011; Chesson, 2000b; Godoy *et al.*, 2014; Saavedra *et al.*, 2017; Spaak & De Laender, 2020; Zhao *et al.*, 2016). We gathered 639 papers, of which 50 contained experimental measurements of niche and fitness differences. These 50 papers contained 29 independent data-sets corresponding to 1018 two species communities (Appendix, section ??, Table.??). Only Veresoglou *et al.* (2018) compute niche and fitness experimentally for multispecies communities. Most other studies either do not contain sufficient information to compute niche and fitness differences in multi-species communities or use data from two-species communities, which ignores higher-order interactions (?). Therefore, for consistency, we did not consider multispecies communities. For each article, we extracted all species-specific growth parameters available (e.g., competition coefficients, sensitivity, intrinsic growth rates, invasion growth rates) and the outcome of species interaction (i.e., coexistence, competitive exclusion, or priority effects). Additionally, we extracted ecological information about the community, such as the taxonomy of the competing species, their co-occurrence (sympatric or allopatric), and methodological information about the experiment, such as the experimental setting (field, greenhouse, or laboratory experiment), the community model fit to the empirical data (Lotka-Volterra model, Annual plant model or no model at all) and the method to measure species growth rates (field observations, growth rates over time or space for time replica, i.e., multiple plots with different initial abundances of competing species) (Appendix, section ??, Table.??). We labeled the taxonomy of the competing species into four different ecological groups: (i) phytoplankton (170 communities), (ii) bacteria and yeast (128 communities), and (iii) terrestrial plants, which we subdivided into annual (459 communities) and (iv) perennial plants (261 communities). We grouped yeast with bacteria as we only found one study using yeast (Grainger *et al.*, 2019a), and due to the size and habitat of both systems. Conversely, thanks to sufficient empirical data, we split terrestrial plants into two subgroups (annual and perennial plants) based on their ecology (i.e., life span).

**Standardising 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 ??, Table.??) (Godwin *et al.*, 2020; Spaak & De Laender, 2020). To compare the different results, we first converted them to the same model-independent definition of niche and fitness differences (Spaak & De Laender, 2020; Spaak *et al.*, 2021). This definition was the only one applicable to all data-sets. Many other definitions were not applicable because they are designed

for a specific community model, such as Beverton-Holt (Beverton & Holt, 1957) (hereafter called the annual plant population model) or Lotka-Volterra community models (Chesson, 2018; Godoy *et al.*, 2014; Saavedra *et al.*, 2017). Another widely used (model agnostic) method by Carroll *et al.* (2011) was not applicable because our data contained considerable net facilitation, which the method does not capture. Importantly, despite being defined on the invasion growth rate, the definition by Spaak & De Laender (2020) converges to the well-known square-root definition when applied to the two-species Lotka-Volterra community model. Additionally, for other community models, this definition is consistent with the typical interpretation of niche and fitness differences (Spaak *et al.*, 2021).

We used the species-specific growth parameters extracted from each article to compute the definition. Indeed, to compute Spaak & De Laender (2020) definition one needs the invasion growth rate  $r_i$ , the intrinsic growth rate  $\mu_i$ , and the no-niche growth rate  $\eta_i$ . The invasion growth rate is the growth rate of the focal species  $i$  when the resident species  $j$  is at its carrying capacity  $N_j^*$ . 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. Given these three growth rates, they define niche differences as  $\mathcal{N}_i = \frac{r_i - \eta_i}{\mu_i - \eta_i}$  and fitness differences as  $\mathcal{F}_i = -\frac{\eta_i}{\mu_i - \eta_i}$ . We use the updated notion for fitness as proposed by Spaak *et al.* (2021), as this leads to the coexistence condition of  $\mathcal{N}_i > \mathcal{F}_i$ . If only the invasion growth rate and the intrinsic growth rates are available, one can produce an estimate of the definition of Spaak & De Laender (2020) (Appendix, section ??, Table.??).

For 719 out of 1018 communities, the authors used a community model, such as the annual plant population dynamics (Levine & HilleRisLambers, 2009), which allows us to simulate all necessary growth rates, and we, therefore, computed niche and fitness differences for these communities. For 234 out of 299 remaining communities, we found the invasion and intrinsic growth rates, but not the no-niche growth rates. For these, we approximated niche and fitness differences by selecting 10 random estimates within a community-specific space (Appendix, section ??, Table.??). For the remaining 65 communities, we found the invasion growth rates and the carrying capacity, but not the no-niche growth rate nor the intrinsic growth rate. Therefore, these were excluded from the analysis, allowing us to analyse 953 communities.

We finally predicted the long-term outcome of the species interactions (coexistence, priority effects, exclusion), given the computed niche and fitness differences. Precisely, a species  $i$  is predicted to persist when  $\mathcal{N}_i > \mathcal{F}_i$ , while a species  $j$  is expected to go extinct when  $\mathcal{N}_j < \mathcal{F}_j$  (Spaak *et al.*, 2021). Coexistence between two species  $i$  and  $j$  is predicted when the inferior competi-

tor (species with minimal  $\mathcal{F}$ , here species  $j$ , for instance) respects the persistence condition  $\mathcal{N}_j > \mathcal{F}_j$ . Priority effects is predicted, on the other hand, if  $\mathcal{N} < \mathcal{F}$  for both species and that both species have a negative  $\mathcal{N}$ . The remaining states predict the exclusion of the inferior competitor.

**Clustering.** We applied an automated clustering algorithm to the niche and fitness differences values of the inferior competitor of each community (species with  $\mathcal{F}_i > 0$ ). We used an expectation-maximisation algorithm with Gaussian kernels (mixture.GaussianMixture, EM clustering for Gaussian-mixture models) from the module 'sklearn' version 0.23.2 in python version 3.8.5. The algorithm fits the best gaussian mixture to the data, i.e., each cluster consists of a location (mean of gaussian distribution) and a spread (covariance matrix of gaussian distribution). We first applied the clustering with one to ten clusters to identify the optimal number of clusters (Appendix ??). We computed the AIC, BIC, log-likelihood, and rand-metric for each clustering. According to all metrics, the optimal number of clusters is three. Note that a species is not assigned to a specific cluster, but rather a probability is given that it belongs to each cluster (soft clustering). For species pairs without reported no-niche growth rate, and for which we previously selected 10 random estimates of niche and fitness differences, we compute the probability of belonging to the three clusters for each of these 10 random estimates. Then we assign the overall probability per cluster as the average over these 10 random estimates. To compute the proportion of species pairs (Fig. 3), we randomly assign each species pair to one of the three clusters according to their respective probabilities and then compute the number of species pairs per cluster. This process was repeated 500 times. To understand the distribution of niche and fitness differences (Fig. 2), we used one histogram per cluster with weights according to the probability of belonging to a cluster.

Next, we performed a meta-analysis using the package "metafor" (Viechtbauer, 2010) in R (R Core Team, 2020) to test whether the different clusters represented different ecological or methodological settings: the occurrence (sympatric or asympatric), experimental setting (field, greenhouse or lab cultures), the used population model (Beverton-Holt annual plant model, Lotka-Volterra or no model at all), and how growth rates were assessed (using field observations, space for time replications, i.e., multiple plots with different initial abundances of competing species, or growth rates over time). With one exception, all communities from the same study had identical ecological and methodological formation. With the `escalc()` function, we computed the proportion of species pairs belonging to each cluster within each study and across the empirical data. We use the sampling variances of those proportions as its precision. Then, with the `rma.uni()` function, we fitted linear mixed-effects models, with the estimated pro-

portions of the clusters as effect sizes and the different ecological or methodological settings used as qualitative moderators. These mixed-effects meta-analyses assume that the actual proportion of the clusters differs from study to study, first because of known differences between the ecological settings of the different studies (the qualitative moderators), but also because of unknown and uncontrolled features of the studies that might affect such cluster proportion. The meta-analyses provide estimates of the average cluster proportions for studies with different ecological settings: studied ecological groups, experimental settings, or community models. If there are significant differences in the proportions of any clusters for different ecological settings, the moderator associated with the setting will be significantly different from zero, and the fitted mixed model will predict significantly different proportions for different ecological settings.

## Results

We identify three potential outcomes of species interactions: coexistence, exclusion, and priority effects. Overall, species pairs predicted to coexist differ from other species pairs in their niche differences rather than their fitness differences. A species  $i$  is predicted to persist when  $\mathcal{N}_i > \mathcal{F}_i$ , while a species  $j$  is expected to go extinct when  $\mathcal{N}_j < \mathcal{F}_j$  (Spaak *et al.*, 2021). By comparing these two species, we can therefore conclude that  $\mathcal{N}_i - \mathcal{F}_i > \mathcal{N}_j - \mathcal{F}_j$ . However, from this inequality, we can neither deduce  $\mathcal{N}_i > \mathcal{N}_j$  nor  $\mathcal{F}_i < \mathcal{F}_j$ ; we solely know that at least one of these must be correct. Depending on which of these inequalities is correct,  $\mathcal{N}_i > \mathcal{N}_j$  or  $\mathcal{F}_i < \mathcal{F}_j$ , we may attribute a prediction of coexistence to large niche differences or small fitness differences. Note that we observe no influence of the number of communities in a study on the proportion of predicted long-term outcomes (Fig. ??).

We found that in the empirical data, niche differences are mainly responsible for predictions of coexistence. In general, we have  $\mathcal{N}_i > \mathcal{N}_j$ , but not necessarily  $\mathcal{F}_i < \mathcal{F}_j$ . Across the  $\mathcal{N}$ - $\mathcal{F}$  map, the species pairs were segregated along niche differences (Fig. 1 C) rather than the fitness differences (Fig. 1 A). Species from pairs predicted to coexist had significantly higher niche differences than species from other pairs (median 0.864 and 0.019, Kruskal-Wallis  $p < 1e - 10$ ). However, they had similar fitness differences (median 0.362 and 0.411,  $p = 0.074$ ). Species in pairs with predicted priority effects had lower niche and fitness differences than species predicted to coexist or suffer exclusion (medians -0.259 and 0.107,  $p < 1e - 5$  in all comparisons). While species pairs with priority effects by definition have lower niche differences than pairs predicted to coexist, it is unclear whether they should have lower fitness differences and lower niche differences than species pairs with competitive exclusion. Thus, we conclude that across the ecological groups considered, predicted coexistence is driven

424 by niche differences and not by fitness differences. More- 478  
425 over, niche and fitness differences values also capture the 479  
426 high-level processes at play (positive, negative, or no fre- 480  
427 quency dependence and facilitation). Here, negative fre- 481  
428 quency dependence ( $0 < \mathcal{N} < 1$ ) is the most prevalent 482  
429 process (Fig. 1C), and mostly leads to a prediction of 483  
430 coexistence. Facilitation ( $\mathcal{N} > 1$ ) and positive frequency 484  
431 dependence ( $\mathcal{N} < 1$ ) are less frequent and primarily re- 485  
432 sult in predicted coexistence and exclusion, respectively. 486

433 Nearly 80% of the data clustered into either of two dis- 487  
434 tinct clusters (Fig. 3 B, Fig. 3 A, Appendix ??). These 488  
435 clusters correspond to the two previously observed peaks 489  
436 along the niche differences (Fig. 1C). We refer to them 490  
437 as “low  $\mathcal{N}$ ” (yellow) and “high  $\mathcal{N}$ ” (green). A third 491  
438 cluster, containing less than 20% of the data, represents 492  
439 many data points across the  $\mathcal{N}$ - $\mathcal{F}$  map and a much larger 493  
440 variance of niche differences. We, therefore, call this the 494  
441 “variable  $\mathcal{N}$ ” cluster (purple). Overall, the clusters had 495  
442 very similar fitness differences. 496

443 The existence of mainly two distinct clusters suggests 497  
444 qualitative differences between both. For example, we 498  
445 might expect that a given cluster mainly contains species 499  
446 from a certain ecological group, e.g., annual and peren- 500  
447 nial plants, while the other cluster would be dominated 501  
448 by species from other ecological groups, e.g., phyto- 502  
449 plankton and bacteria/yeast. However, this was not the 503  
450 case (Fig. 3 B). We similarly asked whether these clus- 504  
451 ters are driven by the co-occurrence (sympatric or al- 505  
452 lopatric), experimental setting (field, greenhouse or lab 506  
453 cultures), the used population model (Beverton-Holt an- 507  
454 nual plant model, Lotka-Volterra or no model at all) or 508  
455 how growth rates were assessed (using field observations, 509  
456 space for time replications i.e. multiple plots with differ- 510  
457 ent initial abundances of competing species, or growth 511  
458 rates over time). We found that, in general, the clusters 512  
459 did not differ significantly in any of these ecological or 513  
460 methodological aspects (Fig. 3 C-F). 514  
515  
516

461 Additionally, the bimodal distribution of niche differ- 517  
462 ences is consistent throughout almost all ecological and 518  
463 methodological differences (Fig. 4). Importantly, the 519  
464 existence of precisely two modes and their location is 520  
465 consistent throughout the data-set, one at roughly  $\mathcal{N} = 0$  521  
466 and the other at roughly  $\mathcal{N} = 1$ . The only exception to 522  
467 this phenomenon are perennial plants (panel A), growth 523  
468 methods assessed from observational data (panel D), 524  
469 and communities fitted with a Lotka-Volterra commu- 525  
470 nity model (panel E). Unfortunately, these three groups 526  
471 share considerable overlap, i.e., data from most peren- 527  
472 nial plant systems stems from observational studies to 528  
473 which a Lotka-Volterra community model was fitted. 529  
474 We, therefore, do not know which of these factors is 530  
475 the driver of the uni-modality. We found no comparable 531  
476 bi-modality in the fitness differences data (Appendix, 532  
477 section ??, Fig ??). 533

## Discussion

We used a model-independent definition of niche and fitness differences for 953 empirical species pairs, allowing for the first time a general analysis of species interactions across multiple ecological and methodological settings. We found that, first, for species pairs predicted to coexist, niche differences were higher than for pairs predicted not to coexist (Fig. 1 C). Therefore, our findings show that large niche differences, not small fitness differences, drive coexistence’s prediction. Negative frequency was also the most prevalent process. Second, we identified two main, clearly distinct clusters, corresponding roughly to species pairs predicted to coexist (high niche differences) and pairs for which coexistence was predicted to be absent (low niche differences, Fig. 2 B). Third, these clusters did not differ in ecological or methodological characteristics (e.g., ecological group, experimental setup, natural co-occurrence, population model used, and growth method). Instead, these clusters seemed to be consistent throughout all these differences (Fig. 3 and 4).

### Large niche differences, not small fitness differences, explained predicted species coexistence at a local scale.

Species coexist when niche differences exceed fitness differences. Therefore, one could expect species predicted to coexist to have both higher niche differences and lower fitness differences than other species. Yet, this hypothesis was rejected as we only found evidence for the former (Fig. 1). At a local scale, coexistence in the examined pairs thus seemed to be primarily driven by mechanisms promoting niche differences, e.g., through self-limitation and net positive interactions (Hallett *et al.*, 2018). These results consolidate and expand on findings from primary studies on annual plants (Godoy *et al.*, 2017; Hallett *et al.*, 2018; Levine & HilleRisLambers, 2009; Matias *et al.*, 2018), perennial plants (Adler *et al.*, 2010; Usinowicz *et al.*, 2012), phytoplankton (Narwani *et al.*, 2013; Picoche & Barraquand, 2020), and bacteria (Li *et al.*, 2019). The results also confirm earlier findings that niche differences are usually much stronger than necessary to coexist (Chu & Adler, 2015; Levine & HilleRisLambers, 2009), which is the case here for the species predicted to coexist, i.e., from the high  $\mathcal{N}$  cluster. The few empirical studies not aligned with our results highlight the limitations of studying locally co-occurring species. For instance, Lanuza *et al.* (2018) and Petry *et al.* (2018) found similar findings but stress the importance of fitness differences on a larger scale. Moreover, studies focused on species that are not historically co-occurring found a stronger influence of fitness differences on the outcome of species interactions (Ocampo-Ariza *et al.*, 2018; Zhang & van Kleunen, 2019). We acknowledge the influence of the prevalent use of locally co-occurring species in investigating coexistence mechanisms, which are therefore probably over-represented in our data-set. Our findings are con-

sequently only valid for these communities of the studied ecological groups. Further investigations are needed to understand the drivers of species interactions among species that fail to coexist beyond the local scale. Nevertheless, our results, aligned with previous findings, indicate that niche differences are the main determinant for local coexistence across ecological groups, highlighting the importance of sustaining mechanisms that promote niche differences.

We also found that negative frequency dependence ( $0 < \mathcal{N} < 1$ ) drives most species pairs. 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 *et al.*, 2017). Furthermore, 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 *et al.*, 2018; Armitage & Jones, 2019). However, the prevalence of negative frequency dependence seems to expand through all communities, highlighting the importance of self-regulating mechanisms rather than species interspecific differences (Armitage & Jones, 2019). On the other hand, facilitation and positive frequency dependence were significantly less present. This complementary result supports that not only mechanisms promoting niche difference but specifically intraspecific mechanisms are essential to maintain coexistence.

The niche differences and the corresponding processes we quantified (fig. 1.C) are the net results of multiple underlying mechanisms leading to multiple kinds of species interactions. Thus, the detection of specific interaction types (e.g. positive ones, Adler *et al.* (2018); Picoche & 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 (Adler *et al.*, 2018; Bimler *et al.*, 2018; Choler *et al.*, 2001; Martorell & Freckleton, 2014; Picoche & Barraquand, 2020; Soliveres *et al.*, 2015; Wainwright *et al.*, 2016) do not contradict our result that net facilitation was less frequently observed.

Our predictions of the long-term outcome of species interactions (coexistence, priority effects, exclusion) are based on often short-term experiments or space-for-time substitutions. These predictions will hold as long as the underlying mechanisms are those active during said experiments. However, on long enough time scales, other mechanisms will inevitably emerge (e.g., contamination in a microbial culture, the emergence of a pathogen in a plant). If these changes lead to different species interactions, long-term outcomes can change.

We have focused on species pairs containing few species and a single interaction type per pair. We can there-

fore not be sure that fitness differences would continue to play a minor role for coexistence in communities with more species (Chu & Adler, 2015; Veresoglou *et al.*, 2018; ?) inevitably hosting a more diverse set of species interaction types (Bartomeus *et al.*, 2021; Parmentier *et al.*, 2020), including asymmetric and higher-order interactions (Letten & Stouffer, 2019; Levine *et al.*, 2017; Mayfield & Stouffer, 2017). On the one hand, theory has shown that all else equal, species richness tends not to affect niche differences while increasing fitness differences (Spaak & De Laender, 2021). Fitness differences could hence become more important for coexistence in more diverse communities. On the other hand, Godoy *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.

**Clustered niche differences.** We found two main clusters in the niche and fitness differences map. These clusters can loosely be classified as low niche differences with species pairs not predicted to coexist (Fig. 2, orange) and high niche differences with species pairs predicted to coexist (green). Unsurprisingly, the cluster with high niche differences will consist of species pairs predicted to coexist. However, the existence of such an apparent clustering, the fact that it occurs predominantly along the niche differences axis, and its independence from ecological or methodological differences are surprising (Fig. 3 and 4).

The community diversity within these clusters hints at generalities across ecological groups: species pairs with distinct ecology cannot be distinguished based on their niche and fitness differences signature. This finding is encouraging, as it implies that similar processes drive dynamics in different species pairs. This information can help understand biodiversity and predict environmental impacts across various systems (Soliveres *et al.*, 2015). However, the result that ecological and methodological predictors could not explain these two clusters also reveals a significant challenge: what drives the clustering of high and low niche species pairs?

We offer two hypotheses to explain the existence of these clusters. The first is based on limiting similarity, i.e., that there is a limit to how similar coexisting species can be (MacArthur & Levins, 1967; Meszéna *et al.*, 2006). The coexistence of interacting species depends on the relative size of the niche space, the range of parameters where species have positive growth, and the niche width, the amount of niche space each species occupies. If the niche space is small relative to the niche widths of the interacting species, then there is one optimal strategy that will competitively exclude all other species (Barabás & D’Andrea, 2016; Kremer & Klausmeier, 2017; Pastore *et al.*, 2021). In this scenario, the interacting species have small niche differences and would be part of the low  $\mathcal{N}$  cluster. Conversely, if the niche space is rela-

tively large, many species will coexist with limited overlap, leading to high niche differences between interacting species and consequently including them in the high  $\mathcal{N}$  cluster. In such a setting (large niche space), Pastore *et al.* (2021) performed a virtual evolution experiment of species along a one-dimensional resource axis (niche space) and found that evolution mainly drives coexistence toward large niche differences, which previous work support (MacArthur & Levins, 1967; Slatkin, 1980; Stomp *et al.*, 2004). Thus, interacting species should evolve towards one of these two extreme scenarios, creating two peaks on the niche axis. However, this hypothesis challenges recent findings, suggesting the predominant interaction of evolution with fitness differences rather than niche differences (Germain *et al.*, 2020; Hart *et al.*, 2019; Pastore *et al.*, 2021). The second hypothesis is based on lumpy coexistence, a combination between niche theory and neutral theory (Scheffer & van Nes, 2006). Limiting similarity posits that species will eventually self-organise at equidistant positions along a one-dimensional niche axis (Barabás & D’Andrea, 2016; MacArthur & Levins, 1967; Meszéna *et al.*, 2006). Lumpy coexistence describes the transient state before this optimal self-organisation. Species will exist in lumps of species with very similar traits and significant gaps between these lumps of species. Species from different lumps will have dissimilar traits and large niche differences, corresponding to the high  $\mathcal{N}$  cluster. Conversely, species within a lump will have very similar niches and compete almost neutrally with each other, corresponding to the low  $\mathcal{N}$  cluster (Scheffer & van Nes, 2006). These species would not coexist strictly, yet they may co-occur for a very long time in nature.

**Limitations and perspectives.** We present a synthesis of the processes driving the prediction of long-term coexistence. Like any meta-analysis, one can identify 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. With few exceptions, the investigated communities consisted of basal species competing for abiotic resources. Our findings might not apply to higher trophic levels, as research suggests that different coexistence mechanisms drive higher-trophic levels (Shoemaker *et al.*, 2020). A deeper understanding of how two-species coexistence links to multispecies coexistence might give us a better understanding of why niche differences are essential in two-species communities. Second, we have little mechanistic understanding of why species pairs predicted to coexist 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 (Adler *et al.*, 2009; Farrer *et al.*, 2010; Godoy & Levine, 2014; Martorell & Freckleton, 2014), and these mechanisms can be fluctuation-

independent (Armitage & Jones, 2019) or fluctuation-dependant (Hallett *et al.*, 2019). To provide such understanding here would be purely speculative, given our data.

Despite these limitations, the presented analysis suggests clustering of species pairs predicted to coexist and not to coexist, but at the same time, a broad generality within these clusters. A logical next step is therefore to connect these results to biological insights of the considered community types (e.g. traits (Kraft *et al.*, 2015; Maire *et al.*, 2012; Narwani *et al.*, 2013), or historical interactions (Germain *et al.*, 2016; Gilbert & Parker, 2016)). Doing so will contribute to a better understanding of the drivers of coexistence.

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1009 1446.

## 1010 **Statement of authorship**

1011 LB and JS designed the collection of data. LB gathered  
1012 the data, with help from all authors. JS computed the N  
1013 and F. LB analysed the data with inputs from JS and  
1014 FDL. JS performed the clustering. JJ performed the  
1015 meta-analysis. LB and JS wrote the first draft of the  
1016 manuscript, and all authors contributed substantially to  
1017 revisions.

## 1018 **Data accessibility**

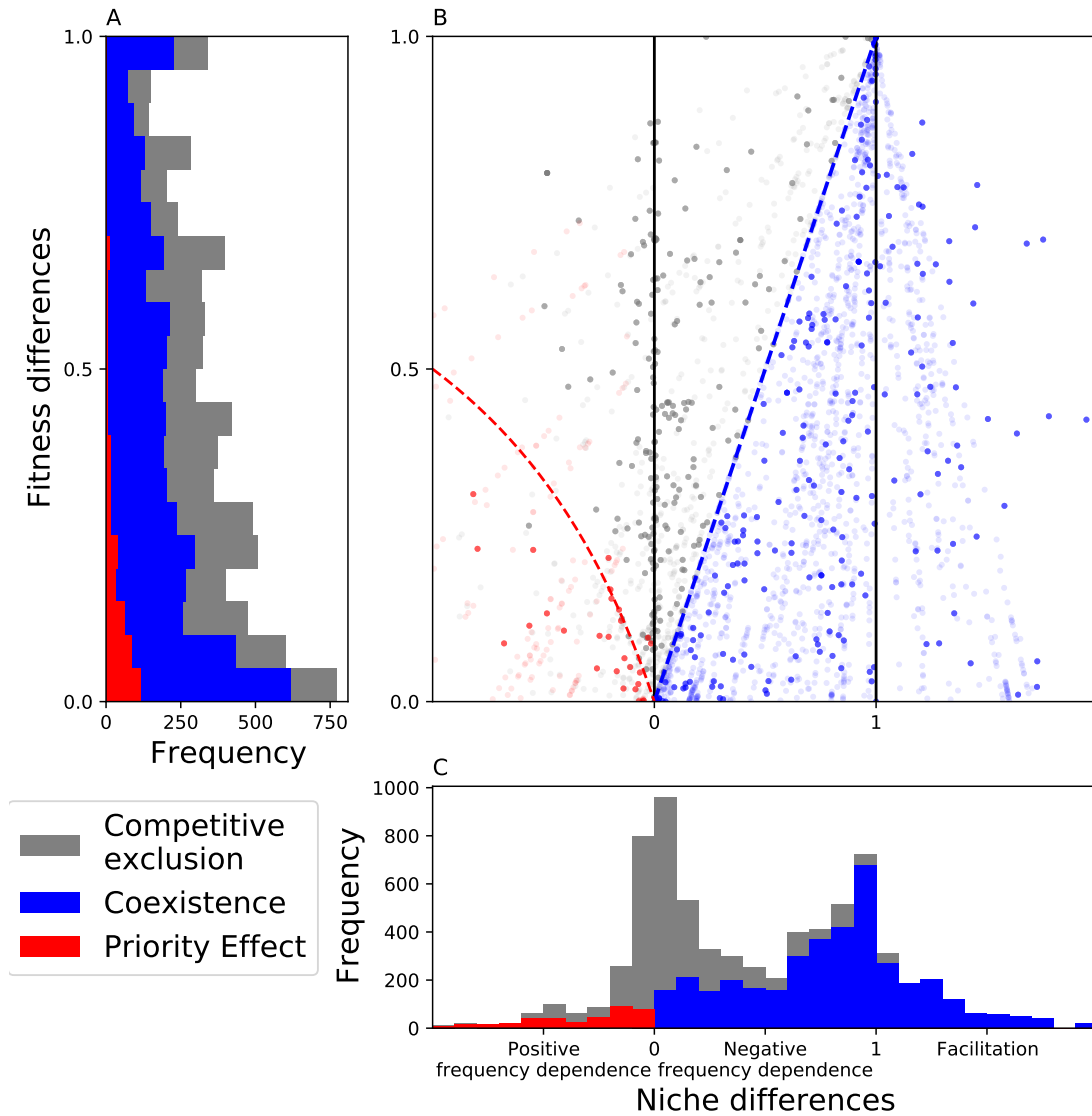
1019 Code and the computed niche and fitness differ-  
1020 ences are available on Github [https://github.com/  
1021 Buchel19844/Meta-analysis\\_NFD](https://github.com/Buchel19844/Meta-analysis_NFD) and Zenodo (Buche  
1022 *et al.*, 2022).

## 1023 **Conflict of Interest**

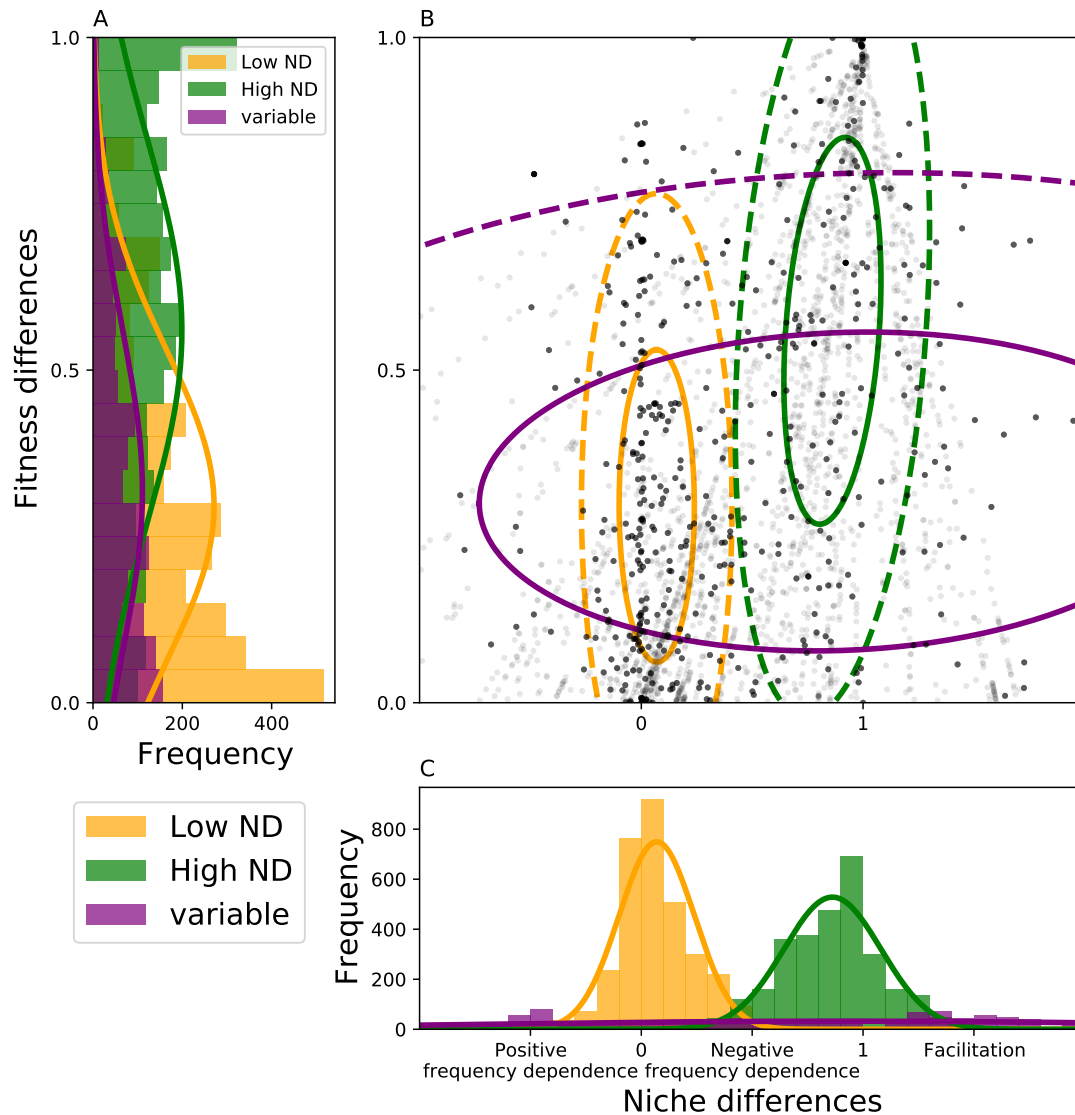
1024 None of the authors have a conflict of interest.

## 1025 **Acknowledgement**

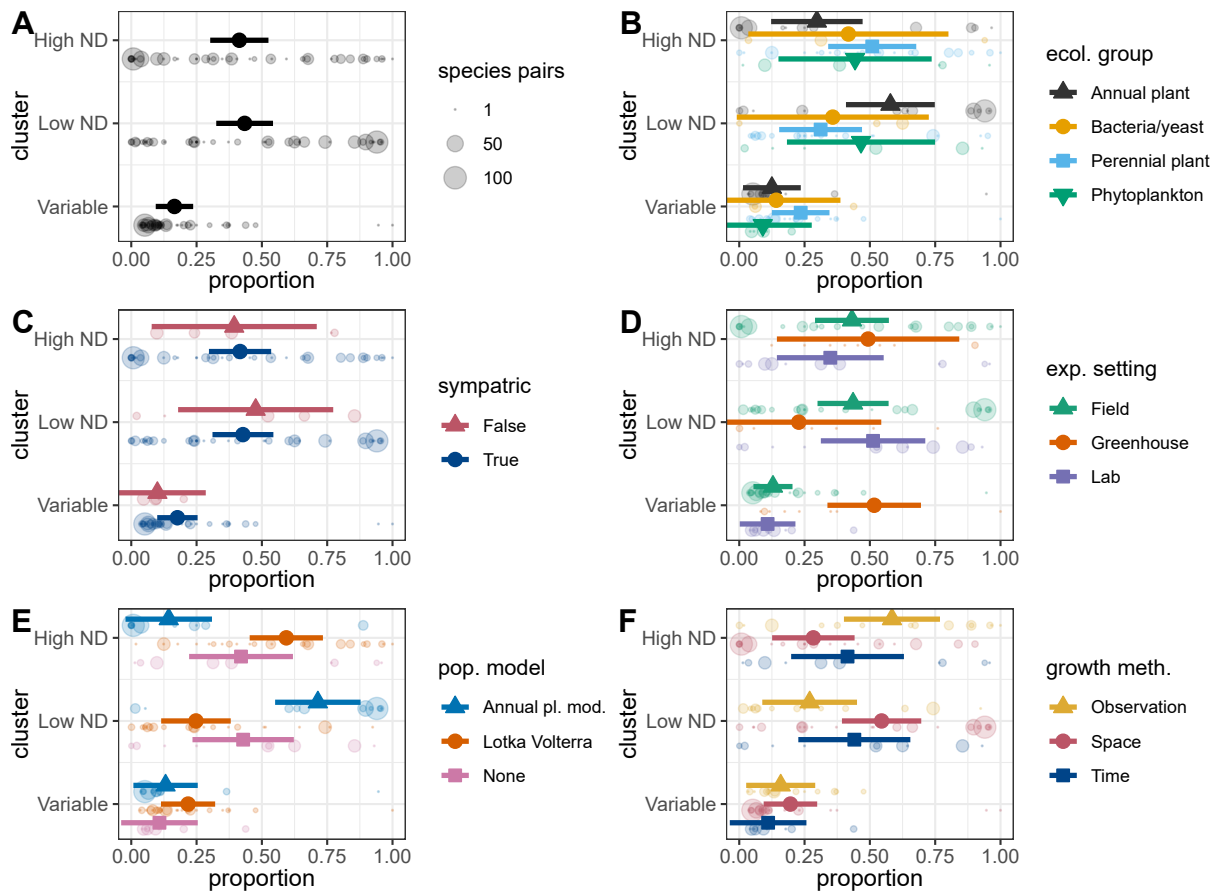
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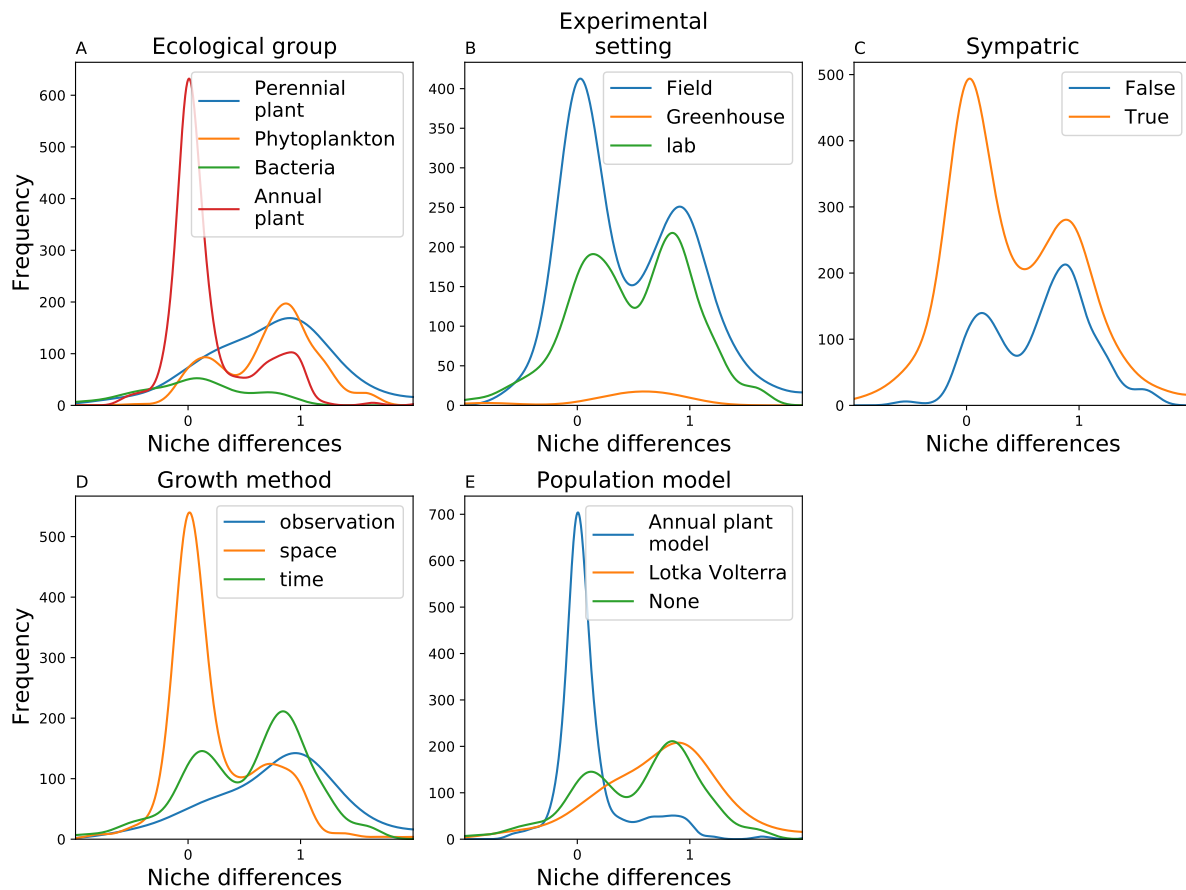
**Fig. 1.** Niche and fitness differences of the inferior competitor for the analysed communities. A - The distribution of fitness differences for communities predicted to coexist (blue), and not-coexist (grey and red) are very comparable. Consequentially, fitness differences do not drive predicted coexistence. B - Distribution of all niche and fitness differences measured empirically. C - Species pairs from communities predicted to coexist (blue) have much higher niche differences than species pairs predicted to not-coexist (grey and red). Additionally, species pairs from communities driven by priority effects (red) have lower niche differences than species pairs from communities driven by competitive exclusion (grey). We, therefore, conclude that niche differences drive the prediction of coexistence. In panel B, the light grey dots represent estimates of niche and fitness differences (10 random estimates within a community-specific space) for empirical data (234 communities) where only invasion and intrinsic growth rate were known (see methods and Appendix, section ??, Table.??). The blue dashed line corresponds to the coexistence line; species pairs below this line persist. The red dashed line delimits the region for priority effects.



**Fig. 2.** Species pairs group in three clusters. In panel B, we group the niche and fitness differences into these three clusters. The ellipses show one, two, and three times the co-variances, containing 68, and 95% data points within each cluster. The purple cluster contains less than 20% of the data (many outside the plotted range). The green and orange clusters, respectively, contain about 40% of the data. A - Projection of the clusters to the fitness differences only. The fitness differences of the different clusters overlap substantially, indicating that fitness differences are not essential to the clustering. C - Projection of the clusters to the niche differences only. The green and orange clusters barely overlap, indicating that the sole knowledge of niche differences would be sufficient to cluster these two. We, therefore, conclude that niche differences drive the clustering. The x-axis from panel A and the y-axis from panel C differ from the corresponding panels in figure 1 because we do not stack the histograms in this figure but did in the previous.



**Fig. 3.** Proportion of species pairs belonging to the different clusters (A–C Fig. 2) obtained for different studies (semi-transparent points), and average proportions of the different clusters obtained through meta-analyses of the individual studies with error bars as confidence intervals (computed with the package “metafor” (Viechtbauer, 2010) in R (R Core Team, 2020)). In panel A, we represent the proportions obtained through random effects models of all the studies:  $41 \pm 6\%$  of species pairs belong to cluster A,  $44 \pm 6\%$  belong to cluster B, and  $16 \pm 4\%$  belong to cluster C. In panels B–F, we represent proportions obtained through mixed-effects models considering respectively as moderators the ecological group of the species pairs (panel B), whether the species pairs are or are not sympatric (panel C), the experimental setting of the study (panel D), the employed population model (panel E), and the growth method (panel F, here divided between field observations, growth rates over time or space for time replica, i.e., multiple plots with different initial abundances of competing species). Generally, these factors have no significant effect on the proportion of species pairs in the different clusters, except for the factors “greenhouse” (panel D) and “annual plant community model” (Panel E). Thus, studies of different ecological groups, of sympatric or non-sympatric species pairs, or with different experimental settings, population models, or growth methods would not differ in the proportion of species pairs that belong to each cluster.



**Fig. 4.** Distribution of niche differences estimated by a Gaussian kernel density estimation for different ecological groups (A), experimental settings (B), co-occurrence status (C), growth methods (D), and population models (E). Almost all subsets of the data show a bimodal distribution of niche differences with peaks at similar locations as from the entire data-set (Figure 2 C). Thus, the bimodal distribution of niche differences is a general pattern spanning different ecological and empirical settings.