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## **Journal of Ecology**

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

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1. Background: Understanding the drivers of species 43 coexistence is essential in ecology. Niche and fitness differences (i.e, how species limit themselves com-<sup>44</sup> pared to others and species' differences in competi-<sup>45</sup> tive ability, respectively) permit studying the conse-<sup>46</sup> quences of species interactions. Yet, the multitude  $_{47}$ of methods to compute niche and fitness differences 48 hampers cross-community comparisons. Such shortcoming leaves a gap in our understanding of the natural drivers of species coexistence and whether niche 51 or/and fitness differences capture them.

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2. Analysis: Here, we standardised niche and fit-53 ness differences across 953 species pairs to investigate species coexistence across ecological groups and  $^{\ 54}$ methodological settings (experimental setup, natural <sup>55</sup> co-occurrence, population model used, and growth 56 method). Using data gathered from 29 empirical pa- 57 pers, 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 methodologi-  $^{\rm 62}$ 63 cal settings drive these clusters.

3. Results: Species pairs predicted to coexist have <sup>64</sup> larger niche differences but not smaller fitness dif- 65 26 ferences than species pairs predicted not to coexist. 66 27 Also, species pairs group into two clear clusters along 67 the niche difference axis: those predicted to coexist 68 29 and those that are not. Surprisingly, ecological or  $_{69}$ 30 methodological settings do not drive these clusters. 4. Synthesis: Overall, our results show that species coexistence is mainly influenced by mechanisms act-72 ing on niche differences, highlighting the importance of sustaining mechanisms that promote niche differ-<sup>73</sup> ences to maintain species coexistence. In addition, our results provide evidence that communities pre-<sup>75</sup> dicted to coexist differ from those that are not in 76 ways that transcend their ecological grouping.

Coexistence | modern coexistence theory | ecologi- 81 40 cal groups| methodological settings| meta-analysis| 82 41 species interactions | clustering 42 83

## 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 &

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De Laender, 2020). Competitive exclusion (coexistence) 141 84

occurs when species pairs cannot (can) persist together, 142 85

irrespective of their initial abundance. Priority effects 143 86

involve exclusion dependent on initial abundance (Ke & 144 87 Letten, 2018; Mordecai, 2011).

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Niche and fitness differences have been applied in the  $^{\rm 146}$ 89 past to synthesise the causes and consequences of species <sup>147</sup> 90 interactions (e.g.Adler et al. (2007); Godoy et al. (2014); 148 91 Godoy & Levine (2014); Narwani *et al.* (2013)). How-<sup>149</sup> 92 ever, their use comes with a significant limitation: there <sup>150</sup> 93 is not a generally accepted method on how to measure <sup>151</sup> 94 niche and fitness differences (Godwin et al., 2020; Song<sup>152</sup> 95 et al., 2019). Instead, there are, at present, eleven dif-<sup>153</sup> 96 ferent methods to assess niche and fitness differences <sup>154</sup> 97 (Koffel et al., 2021; Spaak & De Laender, 2020). Many <sup>155</sup> 98 of these methods are tailored to a specific commu-<sup>156</sup> 99 nity model and, consequentially, have only been applied <sup>157</sup> 100 to ecological groups, which these models well describe <sup>158</sup> 101 (Bimler et al., 2018; Godoy, 2019). This specificity has <sup>159</sup> 102 hampered cross-community comparison. Recently, we <sup>160</sup> 103 developed a method to assess niche and fitness differ-<sup>161</sup> 104 ences (Spaak & De Laender, 2020; Spaak et al., 2021), 162 105 which allows computing niche and fitness differences in <sup>163</sup> 106 a standardised way or converting available data into a <sup>164</sup> 107 common currency. Given this method, it is now pos-<sup>165</sup> 108 sible to use niche and fitness differences as a common <sup>166</sup> 109 currency across multiple ecological groups to ask what <sup>167</sup> 110 permits or hampers species coexistence (Germain *et al.*, <sup>168</sup> 111 2016; Grainger et al., 2019b; Narwani et al., 2013). 169 112

In principle, coexistence can occur when niche differ-113 ences (promoting coexistence) are large, when fitness 114 differences (hampering coexistence) are small, or when 115 both occur. The importance of the former for coex-116 istence has been demonstrated (mostly in plants) in 117 both semi-natural (Adler et al., 2010, 2018; Armitage 118 & Jones, 2019; Chu & Adler, 2015; Godoy et al., 2017) 119 and experimental communities (Li et al., 2019; Mathias 120 & Chesson, 2013; Narwani et al., 2013). However, small 121 fitness differences have also been found to promote the prediction of coexistence (Chu & Adler, 2015). Thus, 123 it is not clear what drives the prediction of coexistence 124 in natural systems: fitness differences, niche differences, 125 or both. Therefore, the first outstanding question is 182 126 whether, across multiple ecological groups, large niche 183 127 difference, small fitness difference, or both explain pre-  $_{\scriptscriptstyle 184}$ 128 dicted coexistence. 129 185

Next, we might ask whether there is a gradual or abrupt 186 130 change in how species predicted to coexist or not interact 187 131 within each other. Specifically, if species pairs predicted 188 132 to coexist differ from the ones predicted to not coexist 189 133 only in the relative strength of these underlying species 190 134 interactions, then we would expect a gradual change of 191 135 niche and fitness differences from coexistence to compet- 192 136 itive exclusion. Conversely, if predicted coexistence is 193 137 driven, at least partially, by fundamentally different un- 194 138 derlying species interactions, then we expect a different 195 139 distribution of niche or fitness differences for coexist- 196 140

fer 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 speciesinteraction 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

ing communities than for non-coexisting communities.

For example, neutrally co-occurring species pairs dif-

## Methods

factors driving niche differences.

**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  $14^{th}$  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 "stabiliseing 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 254 differences experimentally using one of the eleven defi-255 nitions were considered. Out of the eleven definitions, 256 seven were used empirically (Bimler et al., 2018; Car-257 roll et al., 2011; Chesson, 2000b; Godoy et al., 2014; 258 Saavedra et al., 2017; Spaak & De Laender, 2020; Zhao 259 et al., 2016). We gathered 639 papers, of which 50 con- 260 tained experimental measurements of niche and fitness 261 differences. These 50 papers contained 29 independent 262 data-sets corresponding to 1018 two species communi- 263 ties (Appendix, section ??, Table.??). Only Veresoglou 264 et al. (2018) compute niche and fitness experimentally 265 for multispecies communities. Most other studies either 266 do not contain sufficient information to compute niche 267 and fitness differences in multi-species communities or 268 use data from two-species communities, which ignores  $_{269}$ higher-order interactions (?). Therefore, for consistency, 270 we did not consider multispecies communities. For each 271 article, we extracted all species-specific growth parame-  $_{\scriptscriptstyle 272}$ ters available (e.g., competition coefficients, sensitivity,  $_{\scriptscriptstyle 273}$ intrinsic growth rates, invasion growth rates) and the 274 outcome of species interaction (i.e., coexistence, com-275 petitive exclusion, or priority effects). Additionally, we 276 extracted ecological information about the community, 277 such as the taxonomy of the competing species, their co- $_{278}$ occurrence (sympatric or allopatric), and methodologi-279 cal information about the experiment, such as the exper-  $_{\scriptscriptstyle 280}$ imental setting (field, greenhouse, or laboratory exper-  $_{_{281}}$ iment), 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  $\frac{284}{284}$ 283 (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) phy-  $^{\scriptscriptstyle 288}$ toplankton (170 communities), (ii) bacteria and yeast  $^{\scriptscriptstyle 289}$ 290 (128 communities), and (iii) terrestrial plants, which we subdivided into annual (459 communities) and (iv)  $^{291}$ perennial plants (261 communities). We grouped yeast  $^{\scriptscriptstyle 292}$ with bacteria as we only found one study using yeast  $^{\scriptscriptstyle 293}$ (Grainger *et al.*, 2019a), and due to the sise and habitat  $^{294}$ of both systems. Conversely, thanks to sufficient empir-<sup>295</sup> ical data, we split terrestrial plants into two subgroups  $^{296}$ (annual and perennial plants) based on their ecology<sup>297</sup> 298 (i.e., life span). 299

**Standardiseing niche and fitness differences.** For the <sup>300</sup> 29 papers collected, the empirically measured niche and <sup>301</sup> fitness differences were computed by different definitions <sup>302</sup> and are therefore not directly comparable (Appendix, <sup>303</sup> section ??, Table.??) (Godwin *et al.*, 2020; Spaak & <sup>304</sup> De Laender, 2020). To compare the different results, we <sup>305</sup> first converted them to the same model-independent def- <sup>306</sup> inition of niche and fitness differences (Spaak & De Laen- <sup>307</sup> der, 2020; Spaak *et al.*, 2021). This definition was the <sup>308</sup> only one applicable to all data-sets. Many other def- <sup>309</sup> initions were not applicable because they are designed <sup>310</sup>

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  $N_i^*$ . 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. 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-

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tor (species with minimal  $\mathcal{F}$ , here species j, for instance) <sup>368</sup> respects the persistence condition  $\mathcal{N}_j > \mathcal{F}_j$ . Priority ef- <sup>369</sup> fects is predicted, on the other hand, if  $\mathcal{N} < \mathcal{F}$  for both <sup>370</sup> species and that both species have a negative  $\mathcal{N}$ . The re- <sup>371</sup> maining states predict the exclusion of the inferior com- <sup>372</sup> petitor. <sup>373</sup>

374 Clustering. We applied an automated clustering algo-375 317 rithm to the niche and fitness differences values of the  $_{376}$ 318 inferior competitor of each community (species with 377 319  $\mathcal{F}_i > 0$ ). We used an expectation-maximisation algo- $_{378}$ 320 rithm with Gaussian kernels (mixture. Gaussian Mixture,  $_{379}$ 321 EM clustering for Gaussian-mixture models) from the 380 322 module 'sklearn' version 0.23.2 in python version 3.8.5.  $_{381}$ 323 The algorithm fits the best gaussian mixture to the data, 382 324 i.e., each cluster consists of a location (mean of gaussian  $_{383}$ 325 distribution) and a spread (covariance matrix of gaus-326 sian distribution). We first applied the clustering with  $_{385}$ 327 one to ten clusters to identify the optimal number of 328 clusters (Appendix  $\ref{appendix}$  ). We computed the AIC, BIC, log-likelihood, and rand-metric for each clustering. Ac-  $^{386}$ 329 330 cording to all metrics, the optimal number of clusters is 387 331 three. Note that a species is not assigned to a specific 388 332 cluster, but rather a probability is given that it belongs 389 333 to each cluster (soft clustering). For species pairs with- 390 334 out reported no-niche growth rate, and for which we pre- 391 335 viously selected 10 random estimates of niche and fitness 392 336 differences, we compute the probability of belonging to 393 337 the three clusters for each of these 10 random estimates. 394 338 Then we assign the overall probability per cluster as the 395 339 average over these 10 random estimates. To compute the 396 340 proportion of species pairs (Fig. 3), we randomly assign <sup>397</sup> 341 each species pair to one of the three clusters accord-398 342 ing to their respective probabilities and then compute 399 343 the number of species pairs per cluster. This process 400 344 was repeated 500 times. To understand the distribu- 401 345 tion of niche and fitness differences (Fig. 2), we used 402 346 one histogram per cluster with weights according to the 403 347 probability of belonging to a cluster. 404

Next, we performed a meta-analysis using the pack- 405 349 age "metafor" (Viechtbauer, 2010) in R (R Core Team, 406 350 2020) to test whether the different clusters represented 407 351 different ecological or methodological settings: the co-408 352 occurrence (sympatric or asympatric), experimental set- 409 353 ting (field, greenhouse or lab cultures), the used popula- 410 354 tion model (Beverton-Holt annual plant model, Lotka- 411 355 Volterra or no model at all), and how growth rates were 412 356 assessed (using field observations, space for time repli-413 357 cations, i.e., multiple plots with different initial abun-414 358 dances of competing species, or growth rates over time). 415 359 With one exception, all communities from the same 416 360 study had identical ecological and methodological in-417 361 formation. With the escalc() function, we computed 418 362 the proportion of species pairs belonging to each cluster 419 363 within each study and across the empirical data. We 420 364 use the sampling variances of those proportions as its 421 365 precision. Then, with the rma.uni() function, we fit- 422 366 ted linear mixed-effects models, with the estimated pro- 423 367

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  $\mathcal{N}_i > \mathcal{N}_i$  nor  $\mathcal{F}_i < \mathcal{F}_i$ ; 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

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

487 Nearly 80% of the data clustered into either of two dis-  $_{\scriptscriptstyle 488}$ tinct clusters (Fig. 3 B, Fig. 3 A, Appendix ??). These 489 clusters correspond to the two previously observed peaks  $_{_{490}}$ along the niche differences (Fig. 1C). We refer to them  $_{401}$ as "low  $\mathcal{N}$ " (yellow) and "high  $\mathcal{N}$ " (green). A third  $_{_{492}}$ cluster, containing less than 20% of the data, represents  $_{\scriptscriptstyle 493}$ many data points across the  $\mathcal{N}$ - $\mathcal{F}$  map and a much larger 494 variance of niche differences. We, therefore, call this the  $_{495}$ "variable  $\mathcal{N}$ " cluster (purple). Overall, the clusters had  $_{_{496}}$ very similar fitness differences. 497

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

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

## Discussion

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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 stud- 591 534 ied ecological groups. Further investigations are needed 592 535 to understand the drivers of species interactions among 593 536 species that fail to coexist beyond the local scale. Never- 594 537 theless, our results, aligned with previous findings, indi- 595 538 cate that niche differences are the main determinant for 596 539 local coexistence across ecological groups, highlighting 597 540 the importance of sustaining mechanisms that promote 598 541 niche differences. 542 590

We also found that negative frequency dependence (0 < 600543  $\mathcal{N} < 1$ ) drives most species pairs. Our results align with <sup>601</sup> 544 earlier findings in food web theory showing that nega-602 545 tive frequency dependence should be present in up to 603 546 90% of interacting species (Barabás et al., 2017). Fur-604 547 thermore, in annual and perennial plants, intraspecific 605 548 competition was previously found to be on average 1.5 <sup>606</sup> 549 and four to five times larger than interspecific competi- 607 550 tion, respectively (Adler et al., 2018; Armitage & Jones, 608 551 2019). However, the prevalence of negative frequency 552 dependence seems to expand through all communities, 553 610 highlighting the importance of self-regulating mecha-554 nisms rather than species interspecific differences (Ar-<sup>611</sup> 555 612 mitage & Jones, 2019). On the other hand, facilitation 556 and positive frequency dependence were significantly less 557 present. This complementary result supports that not 558 615 only mechanisms promoting niche difference but specif-559 ically intraspecific mechanisms are essential to maintain  $^{\rm 616}$ 560 coexistence. 561

The niche differences and the corresponding processes we 562 quantified (fig. 1.C) are the net results of multiple un-563 derlying mechanisms leading to multiple kinds of species 564 interactions. Thus, the detection of specific interaction 565 622 types (e.g. positive ones, Adler *et al.* (2018); Picoche 566 & Barraquand (2020)) in a community does not guar- $\frac{624}{624}$ 567 antee specific processes (e.g. facilitation) will emerge in  $\frac{1}{625}$ 568 that community. A corollary of this is that our analysis  $\frac{2}{626}$ 569 gives no information about the prevalence of, for exam- $\frac{1}{627}$ 570 ple, positive, asymmetric, or correlated species interac-571 629 tions – it only reflects the net result of such interactions. 620 Thus, findings that positive interactions can be abun-573 dant in nature (Adler et al., 2018; Bimler et al., 2018; 574 Choler et al., 2001; Martorell & Freckleton, 2014; Pic-575 632 oche & Barraquand, 2020; Soliveres *et al.*, 2015; Wain-576 wright et al., 2016) do not contradict our result that net 577 facilitation was less frequently observed. 578

Our predictions of the long-term outcome of species in-579 teractions (coexistence, priority effects, exclusion) are 637 580 based on often short-term experiments or space-for-time 638 581 substitutions. These predictions will hold as long as the  $_{639}$ 582 underlying mechanisms are those active during said ex- $_{640}$ 583 periments. However, on long enough time scales, other 641 584 mechanisms will inevitably emerge (e.g., contamination 642 585 in a microbial culture, the emergence of a pathogen in  $_{\scriptscriptstyle 643}$ 586 a plant). If these changes lead to different species inter-  $_{644}$ 587 actions, long-term outcomes can change. 588 645

We have focused on species pairs containing few species 646 and a single interaction type per pair. We can there- 647

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 over- 705 648 lap, leading to high niche differences between interact-706 649 ing species and consequently including them in the high 707 650  $\mathcal{N}$  cluster. In such a setting (large niche space), Pas-708 651 tore et al. (2021) performed a virtual evolution exper-709 652 iment of species along a one-dimensional resource axis 710 653 (niche space) and found that evolution mainly drives 711 654 coexistence toward large niche differences, which previ-712 655 ous work support (Macarthur & Levins, 1967; Slatkin, 713 656 1980; Stomp et al., 2004). Thus, interacting species 714 657 should evolve towards one of these two extreme sce-715 658 narios, creating two peaks on the niche axis. However, 716 659 this hypothesis challenges recent findings, suggesting the 717 660 predominant interaction of evolution with fitness dif-718 661 ferences rather than niche differences (Germain et al., 662 2020; Hart et al., 2019; Pastore et al., 2021). The sec-663 ond hypothesis is based on lumpy coexistence, a combi-664 nation between niche theory and neutral theory (Schef-<sup>720</sup> 665 fer & van Nes, 2006). Limiting similarity posits that <sup>721</sup> 666 species will eventually self-organise at equidistant po-722 667 sitions along a one-dimensional niche axis (Barabás & 723 668 D'Andrea, 2016; Macarthur & Levins, 1967; Meszéna<sup>724</sup> 669 et al., 2006). Lumpy coexistence describes the transient <sup>725</sup> 670 state before this optimal self-organiseation. Species will <sup>726</sup> 671 exist in lumps of species with very similar traits and sig-<sup>727</sup> 672 nificant gaps between these lumps of species. Species 728 673 from different lumps will have dissimilar traits and large <sup>729</sup> 674 niche differences, corresponding to the high  $\mathcal{N}$  cluster.<sup>730</sup> 675 Conversely, species within a lump will have very similar <sup>731</sup> 676 niches and compete almost neutrally with each other, <sup>732</sup> 677 corresponding to the low  $\mathcal{N}$  cluster (Scheffer & van Nes, <sup>733</sup> 678 2006). These species would not coexist strictly, yet they <sup>734</sup> 679 735 may co-occur for a very long time in nature. 680 736

Limitations and perspectives. We present a synthesis of 737 the processes driving the prediction of long-term coexis-738 tence. Like any meta-analysis, one can identify several 739 limitations. First, our results are only valid for the eco-740 logical groups represented in the data, and other ecolog-741 ical groups may behave differently than the ones consid-742 ered here. With few exceptions, the investigated com-743 munities consisted of basal species competing for abi-744 otic resources. Our findings might not apply to higher 745 trophic levels, as research suggests that different coex-746 istence mechanisms drive higher-trophic levels (Shoe-747 maker et al., 2020). A deeper understanding of how 748 two-species coexistence links to multispecies coexistence 749 might give us a better understanding of why niche dif-750 ferences are essential in two-species communities. 751 Second, we have little mechanistic understanding of why 752 species pairs predicted to coexist exhibit higher niche 753 differences, leading to a prevalence of negative frequency 754 dependence. Various mechanisms can be responsible 755 for this result, including mechanisms driven by spe-756 cific organismal traits (Gallego et al., 2019; Kraft et al., 757 2015), phenological traits (Adler *et al.*, 2009; Farrer 758 et al., 2010; Godoy & Levine, 2014; Martorell & Freck- 759 leton, 2014), and these mechanisms can be fluctuation-760

independent (Armitage & Jones, 2019) or fluctuationdependant (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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#### Statement of authorship 1010

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

#### Data accessibility 1018

Code and the computed niche and fitness differ-1019 ences are available on Github https://github.com/ 1020 Buchel9844/Meta-analysis NFD and Zenodo (Buche 1021 et al., 2022). 1022

#### Conflict of Interest 1023

None of the authors have a conflict of interest. 1024

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**Fig. 1.** Niche and fitness differences of the inferior competitor for the analised 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 drive not-coexist (grey and red). Additionally, species pairs from communities driven by priority effects (red) have lower niche differences than species pairs from communities drive predicted to 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 cluster 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.