

Ecological versatility and the assembly of multiple competitors: cautionary notes for assembly inferences

Victor Saito, Fabien Laroche, Tadeu Siqueira, Sandrine Pavoine

▶ To cite this version:

Victor Saito, Fabien Laroche, Tadeu Siqueira, Sandrine Pavoine. Ecological versatility and the assembly of multiple competitors: cautionary notes for assembly inferences. Ecology, 2018, 99 (5), pp.1173-1183. 10.1002/ecy.2197 . hal-02551812

HAL Id: hal-02551812 https://hal.science/hal-02551812

Submitted on 23 Apr 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1	Running head: Assembly of multispecies communities
2	Ecological versatility and the assembly of multiple competitors: cautionary notes for
3	assembly inferences
4	Victor S. Saito ^{a,b} , Fabien Laroche ^c , Tadeu Siqueira ^d , Sandrine Pavoine ^b
5	^a Departamento de Ciências Ambientais - DCAm and Programa de Pós-Graduação em Ecologia e Recursos,
6	Universidade Federal de São Carlos, São Carlos SP, Brazil, VSS E-mail: victor.saito@gmail.br
7	^b Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR7204), Sorbonne Universités, MNHN,
8	CNRS, UPMC, CP51, 43-61 rue Buffon, 75005, Paris, France, SP E-mail : sandrine.pavoine@mnhn.fr
9	^c Irstea, UR EFNO, F-45290 Nogent-sur-Vernisson, France, FL E-mail: fabien.laroche@irstea.fr
10	^d Universidade Estadual Paulista (UNESP), Instituto de Biociências, Rio Claro, Brazil, TS E-mail:
11	tsiqueira@rc.unesp.br
12	*Corresponding author: victor.saito@gmail.com
13	Full address : Rodovia Washington Luis, km 235, SP-310, CEP 13565-905, São Carlos, São
14	Paulo, Brazil.
15	
16	
17	
18	
19	
20	
21	
22	
23	
24	
25	

26 ABSTRACT

The role of niche differences and competition is invoked when one finds coexisting species to 27 be more dissimilar in trait composition than expected at random in community assembly 28 29 studies. This approach has been questioned as competition has been hypothesized to either 30 lead to communities assembled by similar or dissimilar species, depending on whether species similarity reflects fitness or niche differences, respectively. A current problem is that 31 32 the arguments used to draw relationships between competition and species similarity are based on pairwise theoretical examples, while in nature competition can occurs among a 33 34 constellation of species with different levels of versatility in resources used. By versatility we mean the documented ability of some species to escape competition for commonly used 35 resources by changing for marginal and unused resources. Thus, a versatile species will have 36 37 the ability to decrease niche overlap with all other species when facing strong competitors. 38 When these species are embedded in multiple interactions the role of pairwise niche and fitness differences could be reduced due to indirect effects and thus competition would not be 39 detectable. Here we developed a coexistence theory where competition occurs simultaneously 40 among multiple species with different levels of versatility and then used it in a simulation to 41 unravel patterns of species similarity during community assembly. We found that simulated 42 communities can be assembled by species with more, less or equal similarity compared to a 43 null model when using a mean distance based metric (SES.MPD). However, contrasting these 44 45 varied results, we consistently found species overdispersion using a nearest neighbor-based metric (SES.MNTD), even when species differences reflected more directly their competitive 46 abilities than their niche differences. Strong tendency to overdispersion emerged when high 47 ecological versatility promoted large niche differences and enabled coexistence. This is 48 because versatility to use marginal resources compensates possible fitness differences among 49 species. Our findings provide mounting evidence of the important role of minimum niche 50

differences and versatility in resource consumption for species embedded in multiple directand indirect interactions.

53

Keywords: assembly rules, multispecies competition, functional diversity, limiting similarity,
functional versatility, niche theory, clustering, overdispersion.

56

57 INTRODUCTION

It has become common practice in community ecology to assume that communities 58 59 composed of more dissimilar species than expected at random (hereafter species overdispersion) are predominantly assembled by interspecific competition (Weiher and 60 Keddy 1995; Webb 2000; HilleRisLambers et al. 2012; D'Andrea and Ostling 2016). This 61 62 inference is grounded on MacArthur and Levins's (1967) limiting similarity hypothesis, which claims the existence of a limit to the resource use overlap between species for their 63 stable coexistence. Accordingly, communities composed of similar species (hereafter species 64 clustering) are seen as evidence for relaxed competition for resources and strong abiotic 65 filtering selecting phenotypes well adapted to the environment (Weiher and Keddy 1995). 66

After years of intense application of this approach, Mayfield and Levine (2010) 67 challenged it by explaining that species clustering can also be the result of interspecific 68 competition if species similarities (e.g. calculated using morphologic, behavioral, metabolic 69 70 traits) reflect their competitive hierarchy (see also HilleRisLambers et al. 2012; Adler et al. 2013; D'Andrea and Ostling 2016; Cadotte and Tucker 2017). This happens because, in 71 contrast to the traditional view, not all species differences should promote coexistence. 72 According to Chesson (2000), species coexistence depends on two kinds of interspecific 73 differences. First, stabilizing niche differences (hereafter niche differences) favor coexistence 74 by reducing the overlap in resource use between species in time or space, making 75

76 intraspecific competition more intense than interspecific competition (Chesson 1991). 77 Second, species-level average fitness differences (hereafter fitness differences) determine which species will outcompete others in absence of niche differences (Chesson 2000). A 78 79 balance between niche and fitness differences determines stable coexistence and the pairwise coexistence condition is that niche differences must overcome fitness differences (Chesson 80 2000). So, if species similarities relate to their fitness equalities, then one could expect to find 81 82 species clustering around an optimum trait value when competition rules the assembly (Mayfield and Levine 2010). 83

84 Understanding how differences in species morphology, behaviors and strategies influence niche and fitness differences between them is a complex challenge (Godoy et al. 85 2014; Herben and Goldberg 2014; Kraft et al. 2015; D'Andrea and Ostling 2016). Several 86 87 traits can impact both niche and fitness differences, even if the net impact on one is higher 88 than on the other (Kraft et al. 2015). For example, two animal species competing for different prey can have distinct preferences for prey size and taxonomic identity of prey. Differences 89 in taxonomic preferences could favor coexistence through resource partitioning but size 90 preferences could lead to competitive asymmetry given that feeding on larger animals may 91 improve species fitness. Thus, differences in taxonomic and size preferences would 92 contribute to both niche and fitness differences. Therefore, it is not clear whether analyzing 93 94 together traits that drive stabilizing and equalizing mechanisms simultaneously should give 95 clustered, segregated or random patterns.

Beyond the importance of niche and fitness differences for competitive outcomes, two
characteristics of species competition are usually overlooked in community assembly studies.
First, competition generally happens between several species in nature (Pianka 1974), not
only in pairwise situations, as commonly considered in conceptual and experimental
examples (Mayfield and Levine 2010; Chu and Adler 2015). The addition of a third (or more)

101 species to a community composed of two species modifies the competitive network. This happens because three species can experience indirect effects of each other (Levine 1976; 102 Lawlor 1979). For example, let us consider species A, B and C: species A has a direct effect 103 on species B by directly competing for resources, but also has an indirect effect by competing 104 105 with the third species C, which is a common competitor of species A and B – thus the full impact of species A on B would be the sum of the direct and indirect effects. Given that, the 106 107 pairwise coexistence condition -i.e. niche differences must exceed fitness differences (Chesson 2000) – is not the only determinant of species coexistence, as it is also influenced 108 109 by the other species that compose such a community.

Second, one of the most used models of species competition considers that 110 competition occurs over a linear array of resources and each species have a trait that makes 111 112 them able to consume a range of this array of resources (the MacArthur's consumer-resource model, 1970). In this case, trait differences determine the resource use overlap and thus the 113 interaction strength among species (see Fig. 1). However, competition in nature can happens 114 in a different way. In other documented cases, all species will be able to consume one 115 common resource (in general an abundant resource), but they may vary in the ability to 116 consume other resources, changing their dependency on this common resource when facing 117 competition (Liem 1980; 1990; Bellwood et al. 2006). For example, Liem (1980) found that 118 morphological differentiation in mouth apparatus in cichlids determine the ability of species 119 120 to escape competition for common preys (by changing for a different resource) in the presence of strong competitors. In this case, differences in traits impacts their versatility and 121 thus could determine niche differences with all other species simultaneously using the 122 coexistence framework (see Fig. 1 for a schematic explanation of the differences between 123 MacArthur's model and our model considering species versatility). 124

So, based on the potential impact that multispecies competition and species versatility 125 may have on community assembly, we investigated the strength of commonly used metrics of 126 species dispersion (e.g. mean pairwise and nearest neighbor metrics, Weiher and Keddy 127 1995; Webb 2000) to detect signatures of competition under a mechanistic model of 128 competition. We first developed the underlying theory of competition considering species 129 versatility upon Chesson's (2000) coexistence theory and then used it within a simulation 130 131 based on sequential colonization from a species pool. We observed the emergence of species clustering, overdispersion and random patterns in simulated communities fueling the ongoing 132 133 discussion on the use of species dispersion metrics to infer assembly processes.

134

142

135 METHODS

136 Theory development

We used a model to simulate community assembly based on modern coexistence theory and
under multispecies competition (see Appendix S2 in Supporting Information for a detailed
version of the model and proofs). We aimed a reference model that respects Chesson's (2000)
following to the long-term low-density growth rate of a species *i* in a multispecies system
(Eq. 4 in Chesson 2000):

$$\overline{r_i} \approx b_i \left(k_i - \frac{\sum_{s \neq i} k_s}{n-1} \right) + b_i \frac{(1-\rho)}{n-1} D \tag{1}$$

where *n* is the number of species in the system, the *k*s are measures of fitness of individual species, $(\sum_{s\neq i} k_s)/(n-1)$ is the average fitness of the competitors of *i*, ρ is a measure of niche overlap, and *D* is a positive constant. This equation is composed of an equalizing term $b_i \left(k_i - \frac{\sum_{s\neq i} k_s}{n-1}\right)$ (2)

147 and a stabilizing term

$$b_i \frac{(1-\rho)}{n-1} D \tag{3}$$

In this kind of community model, a set of species is said to coexist if all individual species can grow from low density in the community made of the n - 1 other species at equilibrium (i.e. community feasibility).

We started with MacArthur's consumer-resource model where n species compete for mresources (Eqs. 1 and 2 in Chesson 1990):

154
$$\begin{cases} \frac{1}{x_{i}} \frac{dX_{i}}{dt} = b_{i} [\sum_{l=1}^{m} c_{il} w_{l} R_{l} - m_{i}] \\ \frac{1}{R_{l}} \frac{dR_{l}}{dt} = r_{l} \left(1 - \frac{R_{l}}{K_{l}}\right) - \sum_{i=1}^{n} c_{il} X_{i} \end{cases}$$
(4)

where *i* is a consumer species; X_i is population density; R_l is the density of food resource *l*; w_l is the value of one unit of resource *l* to the consumer; c_{il} is the rate at which consumer species *i* captures resource *l* per unit abundance of resource *l*; m_i is the total value of resource that must be harvested per capita for the growth rate to be exactly 0; b_i is a factor converting the resource excess into the per capita growth rate; r_l is the growth rate and K_l the carrying capacity for resource *l*.

Assuming a separation of time scales between resource and consumer dynamics yields (seeAppendix S2):

163
$$\frac{1}{\tilde{X}_i}\frac{d\tilde{X}_i}{dt} = \tilde{b}_i \left[\tilde{k}_i - \sum_{j=1}^n \tilde{\alpha}_{ij} \tilde{X}_j \right]$$
(5)

where \tilde{X}_i and \tilde{b}_i are rescaled quantities corresponding to X_i and b_i from equation (4), \tilde{k}_i is a 164 rescaled quantity corresponding to $\sum_{l=1}^{m} c_{il} w_l R_l - m_i$ in equation (4) and $\tilde{\alpha}_{ij}$ is a rescaled 165 interaction coefficient between species *i* and *j*, comprised between 0 and 1, which 166 corresponds to a resource overlap between the two species (in particular $\tilde{\alpha}_{ii} = 1$). 167 Consider species *i* at low density, and assume that the n - 1 other species can coexist. Then 168 all the other species $j \neq i$ harboring their equilibrium density \tilde{X}_{ii} (second subscript "i" 169 meaning "in the absence of species i"). Then the long-term growth rate at low density of 170 species *i*, $\bar{r_i}$, is obtained by neglecting $\tilde{X_i}$ and setting the $\tilde{X_i}$ s to $\tilde{X_{ii}}$ s in (5): 171

172
$$\bar{r}_i = \tilde{b}_i \left[\tilde{k}_i - \sum_{\substack{j=1\\j\neq i}}^n \tilde{\alpha}_{ij} \tilde{X}_{ji} \right]$$
(6)

To derive an equation for the long-term low-density growth rate of a species in the form of 173 174 Chesson's approximation for multispecies system (Eq. 1), we considered a particular type of interactions among species that reflect species versatility: for all pairs of species $i \neq j$, we 175 assumed that $\tilde{\alpha}_{ii} = \theta_i \theta_i$, where $\theta = (\theta_1, \theta_2, ..., \theta_n)$ is a vector of positive real numbers 176 between 0 and 1. In particular, $\tilde{\alpha}_{ii} = 1$. Empirically, θ can be a measure of resource use 177 restriction or versatility (e.g. Bellwood et al. 2006 used the species distance to the centroid of 178 a multidimensional space of species distances as a measure of versatility). High values of 179 θ means that a species will depend mostly on the common resource all species can consume, 180 while species with low θ will be those with the versatility to use marginal resources when 181 facing competition (see Fig. 1). 182

Importantly, we show in Appendix S2 that any set of interactions of this type can be obtained by adjusting the basic parameters of the model (resource renewal dynamics and consumption vectors), as long as the number of resource types is equal or greater than the number of species. As similar to the MacArthur's model, resource types can be anything that can vary and can be depleted for other species, i.e. seed size ranging from 1 to 100 cm can be considered 100 resources for birds if each size encompasses a resource that provide niche differences and can be limiting:

190
$$\bar{r}_{i} = \tilde{b}_{i} \left(\tilde{k}_{i} - \frac{\theta_{i}}{\left(1 + \sum_{\substack{l=1\\l \neq i}}^{n} \frac{\theta_{l}^{2}}{1 - \theta_{l}^{2}}\right)} \sum_{\substack{j=1\\j \neq i}}^{n} \frac{\theta_{j}}{1 - \theta_{j}^{2}} \tilde{k}_{j} \right)$$
(7)

We now seek to decompose equation (7) into stabilizing and equalizing terms as in Chesson's (2000) framework. To find the stabilizing term, we first looked at the long-term growth rate at low density when all the species have the same fitness \tilde{k} . In this case, only the stabilizing should act on coexistence. When all species have equal fitness, (7) becomes:

195
$$\bar{r}_{i} = \tilde{b}_{i}\tilde{k}\left(1 - \frac{\theta_{i}\sum_{j=1}^{n} \frac{\theta_{j}}{1 - \theta_{j}^{2}}}{1 + \sum_{\substack{l=1\\l \neq i}}^{n} \frac{\theta_{l}^{2}}{1 - \theta_{l}^{2}}}\right)$$
(8)

We now search for the corresponding equalizing term in an additive decomposition as in
Chesson's (2000) framework (Eq. 1 above). Starting from (7), we obtained (see Appendix S2
for detailed proofs) the following final expression for the long-term growth rate of a species:

$$199 \quad \bar{r}_{i} = \tilde{b}_{i} \left(\tilde{k}_{i} - \frac{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}} \tilde{k}_{j}}{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}}} + \frac{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}} \tilde{k}_{j}}{\sum_{j\neq i}^{n} \frac{1-\theta_{j}}{1-\theta_{j}^{2}}} \left(\mathbf{1} - \frac{\sum_{j=1}^{n} \frac{\theta_{i}\theta_{j}}{1-\theta_{j}^{2}}}{1+\sum_{l=1}^{n} \frac{\theta_{l}^{2}}{1-\theta_{l}^{2}}} \right) \right) = \tilde{b}_{i} \left(\tilde{k}_{i} - \bar{k}_{i} + (1-\rho_{i}) \bar{k}_{i} \right)$$
(9)

200 where

201
$$\bar{k}_i = \frac{\sum_{j=1}^n \frac{\theta_j}{1-\theta_j^2}}{\sum_{j=1}^n \frac{\theta_j}{1-\theta_j^2}}$$

202
$$\rho_i = \frac{\theta_i \sum_{j=1}^n \frac{\theta_j}{1-\theta_j^2}}{1 + \sum_{\substack{l=1\\l \neq i}}^n \frac{\theta_l^2}{1-\theta_l^2}}$$

203

We thus retrieved in (9) a stabilizing term with a form consistent with Chesson's (2000)equation (Eq. 1).

The main difference with Chesson's (2000) framework is that \bar{k}_i is not a simple arithmetic mean of the fitness values but a weighted mean, where weights $(\frac{\theta_i}{1-\theta_j^2})$ depend on some interaction effects with other species. Changing interactions among species thus changes the \bar{k}_i . Our theory provides a multispecies extension of the pairwise Chesson's theory in the case when interactions strength among species simultaneously affects in the same direction the competition with all the other species. This is because all species can consume a common

resource, but vary in their versatility to consume other resources (see Fig. 1).

214 Simulation description

To simulate community assembly, we created a species pool with 100 species. For 215 each species we settled values of k_i and θ_i – the parameters of species in our coexistence 216 model (Eq. 9). The values of these species parameters determine niche and fitness differences 217 218 and thus both are necessary to determine coexistence in communities using equation (Eq. 9). Biologically, k_i would be related to one or several morphological, behavioral or other traits 219 that influence species competitive ability. Theta, however, represents a synthetic measure of 220 ecological versatility indicating the extent to which a species depends on a common resource 221 that all other species can consume (see Fig. 1). We calculated fitness differences and niche 222 differences resulting in two species distance matrix, one that represented species niche 223 overlap $(1-\theta_i\theta_i)$ (from 0 to 1) and another that represented competitive differences ($|\tilde{k}_i - \theta_i|^2$) 224 \tilde{k}_i). Subsequent analyses of species similarity were based on these two species distance and 225 not on \tilde{k}_i s and θ_i s directly. So, species competitive ability determines competitive exclusion 226 227 in the lack of niche differences, while species versatility determines the niche overlap among species. 228

We simulated values for parameters k_i and θ_i using the beta distribution, which is a 229 continuous probability distribution defined on [0, 1] with two positive parameters: α and β . 230 We used α and β to control the means of k_i and θ_i values and their variation. It is important to 231 stress that low α values for θ_i means that, overall, species are highly versatile. Controlling the 232 α and β parameters in the beta distribution allowed us to simulate various scenarios for the 233 distribution of fitness and niche differences in the species pool (Fig. 2). Differences between 234 the parameters of the beta distribution (Fig. 2) are due to differences in the way fitness and 235 interaction strength interfere in the model, fitness in an additive manner and interaction 236 strength in a multiplicative manner. 237

Once the species pool was defined, we built the model to simulate community 238 assembly. The model requires a given a priori number of colonization events to occupy a 239 community. The species pool is unchanged so that a single species can try to invade a 240 community several times. The first species is randomly selected from the pool and occupies a 241 community. Then, the model randomly selects a second species to invade the community and 242 applies the coexistence condition (Eq. 9) to decide whether the first and the second species 243 244 can coexist in that community. If these species can coexist, the next (third) invader would be tested using the multispecies coexistence condition (Eq. 9). Subsequent colonizing species 245 246 are tested for the coexistence condition with all species that already coexist there. The process of assembly ends when all the colonization events defined a priori were done. We 247 also simulated scenarios where species have different colonization probabilities depending on 248 their k_i and θ_i , one with a colonization-competition trade-off and another where species that 249 rely mostly on a common resource have higher chance to colonize new patches. However, 250 251 these simulations provided highly similar results to the random dispersal approach. Thus, these are only described in Appendix S3. 252

In this model, when the coexistence condition was not satisfied and the long-term 253 254 growth rate of the invader was negative, then the invader was excluded. If the coexistence was not satisfied and the long-term growth rate of the invader was positive, then the species 255 with the minimum long-term growth rate was excluded and the coexistence condition was 256 tested in the new resulting community. This process was repeated until the coexistence 257 condition was satisfied. We relied on previous work (Tregonning and Roberts 1979; Wilson 258 259 and Lundberg 2004) to assume that the iterative removal of species with negative growth rates provides a reasonable approximation of the equilibrium community. 260

We defined a simulation as each round starting from simulating the species pool to the assembling of 100 communities. So, each simulation has one singular species pool to

assemble 100 communities. A simulation thus ends with a set of 100 communities assembledunder the same conditions.

265

266 **Community metrics**

To analyze the communities, we calculated species richness, beta diversity (Jaccard 267 dissimilarity) and two metrics of species dispersion. Among species dispersion metrics, we 268 269 used the standardized effect size of mean pairwise distances (SES.MPD) and that of the mean distance to the most similar species within communities (SES.MNTD, Webb 2000). We used 270 271 the 'taxa shuffle' null model that randomizes 1,000 times the rows and columns of the species distance matrix. An additional metric of functional dispersion was also calculated. However 272 this metric provided very similar results from SES.MNTD and SES.MPD, so we included 273 274 these results in Appendix S3.

As a first step, we ran 100 simulations, with 100 invasions in each community, for 275 each combination of fitness and niche distributions (Fig. 2). In these simulations, we first 276 applied the species dispersion metrics (SES.MNTD and SES.MPD) to each assembled 277 community, but separately to fitness distances and niche distances. Next, we applied the 278 dispersion metrics to a combined niche and fitness-based distance between species named 279 'overall species distance' and defined as: $\frac{1}{2\max(Fitness \, distance)} + \frac{1}{2\max(Niche \, distance)}$, where 280 maxima are over all species pairs in the species pool. Finally, to simulate studies gathering 281 traits more related to niche or fitness differences among species (see Kraft et al. 2015), we 282 modified the way we defined overall species distances as: 283

284 $\frac{a}{a+b\max(Fitness \, distance)} + \frac{b}{a+b\max(Niche \, distance)}$, where maxima also are over all species pairs in 285 the regional species pool and *a* and *b* are positive parameters. This simulation represents 286 studies gathering different number of traits related to niche differences (larger values of *b*) 287 and fitness differences (larger values of *a*), or also simulates studies where one singular trait relates to both niche and fitness differences but with different weights (e.g. Godoy et al.

289 2014; Kraft et al. 2015). In a second step, we varied the number of colonization events per

community considering 30, 50, 100, 300 and then 500 colonization events.

291

292 **RESULTS**

When communities were assembled by 100 colonization events, we found a positive trend in species richness by increasing the niche differences (and versatility) and the fitness values at the species pool scale (Fig. 3a). Beta diversity was high on average, independently of niche differences and species fitness at the species pool scale (Fig. 3b).

Considering the species dispersion metrics, when species distances were calculated 297 using niche differences only, we found consistent overdispersion (Fig. 3c,d). With larger 298 299 niche differences and higher fitness at the species pool scale, overdispersion tended to be 300 more evident. When species distances were calculated using fitness differences only, we found clustering for most simulations (Fig. 3e,f). The exceptions were a tendency to 301 randomness when mean species k were low at the species pool scale (Fig 3c first boxplots 302 within each color) and when niche differences were high at the species pool scale for the 303 SES.MNTD metric (Fig. 3e, yellow boxplots). When overall species distances were 304 calculated, we found a strong tendency towards overdispersion using the SES.MNTD metric 305 (Fig. 3g), especially when niche differences at the species pool scale were large (species 306 307 where highly versatile) (Fig 3g yellow boxes). The only exception happened when the species pool had small ks values (Fig. 3g, first blue box). 308

When using the SES.MPD metric, results were more variable: 1) overdispersion when species had large niche differences at the species pool (Fig. 3h, yellow boxes) or similarly high *k*s at the species pool (Fig. 3h, third boxes within each color); 2) a tendency to clustering when species *k*s had a U-shaped distribution (Fig. 2h, forth blue and red boxes); 3) random

patterns when species had low or medium *k* and/or niche differences at the species pool (Fig.
314 3h, first and second blue and red boxes).

When varying the weights of niche differences and fitness differences in species 315 overall distance (i.e. varying the parameters a and b when calculating overall distances), we 316 found that the weights strongly impacted dispersion metrics, independently of the species 317 pool properties. For brevity, we only show the results when species have medium niche 318 319 differences and medium ks values at the species pool scale. We found that SES.MNTD was overdispersed even when we gave more weight to fitness differences than niche differences 320 321 (Fig. 4a). There was a tendency towards randomness and clustering when fitness differences were four to five times more important than niche differences (Fig. 4a). Using SES.MPD, we 322 found random patterns when the weights of niche and fitness differences was the same, but 323 324 clustering and overdispersion when there were more weights to fitness and niche differences, 325 respectively (Fig. 4b).

Varying the number of sequential colonization events led to the same general 326 conclusions (Fig .5). For brevity, we only show the results obtained with medium niche 327 differences and fitness values at the species pool scale. Community richness increased with 328 more colonization events, but stabilized after some point (Fig. 5a). Beta diversity decreased 329 with increasing colonization reaching very low levels after 300 and 500 colonization events 330 (Fig. 5b). We found consistent niche overdispersion and fitness clustering (Fig. 5c,d,e,f). 331 332 Using overall species distance we found overdispersion using SES.MNTD with a minimum of 50 colonization events and only randomness using SES.MPD (Fig. 5g,h). Overall, 333 dispersion patterns became more evident with increasing number of colonization events. 334 335

336 **DISCUSSION**

Community assembly studies have the ambitious aim of inferring processes by 337 analyzing similarities in traits or in evolutionary history among species in a given community 338 (Weiher and Keddy 1995; Webb 2000). We show, however, that such approaches can suffer 339 from two types of Achilles' heels when linking patterns to processes. The first is when 340 different processes result in the same pattern. We found that communities containing very 341 similar species – a pattern used to infer environmental filtering (Weiher and Keddy 1995; 342 343 Webb 2000) – can also be the result of competition alone (Mayfield and Levine 2010). The second is when one process leads to different patterns. We found that competition can result 344 345 in communities containing very distinct species (i.e. an overdispersed pattern, as predicted by the traditional framework), but also in communities with clustered (as predicted by Mayfield 346 and Levine 2010) and even random structure. These problems likely arise because we 347 348 simulated communities with the inclusion of two scenarios rarely considered in previous 349 studies: simultaneous competition among multiple competitors (e.g. Godoy et al. 2017) and species with different levels of versatility to exploit marginal resources. These results bring 350 concerns to the use of the traditional community assembly approach, but enabled us to do a 351 step forward in understanding recurrent patterns of communities in nature. 352

Here, we introduced an extension of the pairwise theory of coexistence using a 353 variation of the MacArthur's consumer-resource model (Chesson 1990) that considers species 354 versatility to determine the interaction strength among species. This new model differs in 355 356 important points from the traditional view of competition (Fig. 1) but yield concordant patterns with previous inferences on the impacts of ecological versatility in community 357 assembly. For example, species richness increased with species versatility in the community 358 and in the species pool scale (Bellwood et al. 2006; Belmaker et al. 2012). Additionally, we 359 found that versatility provides important niche differences and promotes coexistence when 360 competitors from the pool are very strong (high fitness), as already suggested for empirical 361

362 communities (e.g. cichlids, Liem 1980). Overall, these concordances from theory and data
363 emphasize the important role that versatility may play in the assembly of natural
364 communities.

Our findings indicate that empirical studies able to separate niche from fitness traits 365 (e.g. Kraft et al. 2015) could have found species overdispersion if species distances reflected 366 niche differences, but clustering if it reflected fitness differences. However, in the case traits 367 368 impact both fitness and niche differences (Adler et al. 2013; Kraft et al. 2015), our results suggest that MPD metrics can also be random. Previous empirical studies indeed found 369 370 clustering and overdispersion using different traits with an overall species clustering, but the interpretation relied on the opposing effects of environmental filtering and limiting similarity 371 (e.g. Swenson and Enquist 2009). Here, we demonstrated how these same patterns can arise 372 373 due to competition only, when fitness have a U-shaped distribution (Fig. 3h). The U-shaped 374 distribution is the only bimodal distribution we used and it demonstrated to promote different patterns compared to when fitness has unimodal distributions. Empirically, traits with 375 bimodal distribution are recurrent in nature (e.g. marine zooplankton and stream biotas with 376 bimodal size distribution [Warwick and Clarke 1984; Poff et al. 1993]). So, as these patterns 377 can be found in nature, it is likely that clustering in some traits (related to competitive ability) 378 and overdispersion in others (related to species versatility) are also possible when 379 competition rules the assembling. 380

The distributions of niche and fitness differences in the species pool had pivotal effects in determining the level of species dispersion, especially in SES.MPD. With large niche differences in the species pool (i.e. species are highly versatile), overdispersion emerged consistently when using overall species distances. This is likely the result of a possible coexistence when most species have large niche differences, independently of their fitness differences (Chu and Adler 2015). A strong tendency towards overall overdispersion

387 also emerged with high fitness at the species pool scale. This contradicts the idea that communities dominated by strong competitors should have clustered patterns (Mayfield and 388 Levine 2010), at least when species vary in their dependency for a common resource. 389 390 Actually we found that, in these cases, species would tend to be high versatile to overcome possible large fitness disadvantages. In a more conservative case, when the species pool has 391 medium fitness values and medium niche differences, overall distance was in most cases 392 393 random (Figs. 2h and 4h). Given the commonness of a bell-shaped distribution of traits in nature (e.g. traits evolving under a Brownian motion commonly result in normal distributions 394 395 around an ancestral trait value, Kraft et al. [2007]), it is not surprising that most studies to 396 date have observed random patterns when analyzing mean distance-based metrics (82% according to a review by Götzenberger et al. [2012]). Thus, we support recent studies 397 398 cautioning the inference of stochastic processes, e.g. random variation in birth and death 399 rates, as the main processes governing communities with random dispersion patterns (Gallien 2017). 400

Besides the cautionary notes, we found one consistent result across most model 401 variations: consistent overdispersion when using the SES.MNTD metric. This finding 402 supports the importance of minimum niche differences between species in stable multispecies 403 communities (Godoy et al. 2017). This is likely because a high ability to escape competition 404 for a common resource will help overshadow the competitive differences with all other 405 406 species (e.g. Liem 1980). After years of criticism (Mayfield and Levine, 2010; Adler et al. 2013; Gallien 2017), we add new evidence that the signature of pairwise niche differences in 407 communities assembled by multispecies competition is the same overdispersion hypothesized 408 409 by Weiher and Keddy (1995), even when indirect effects due to multiple interactions could act to weaken such pattern (Godoy et al. 2017). It is also important to note that Godoy et al 410 (2017) used a different model of competition (an annual plant species model, Godoy et al. 411

2014), but also found the similar pattern of overdispersion. This highlights the general
importance of minimum niche differences even when considering competition in different
ways.

In this recent study, Godoy et al. (2017) also discussed the role of niche differences 415 and intransitivity (rock-paper-scissor dynamic) in maintaining multispecies communities, 416 explaining that both would give similar empirical signals of overdispersion. However, for 417 418 intransitive competition to promote coexistence, species need to differ in their ability to compete for different resources, thus making possible that a superior competitor for resource 419 420 A is worse when competing for resource B (Gallien et al. 2017). However, this scenario cannot arise in our model as competitive ability is a general characteristic, not related to each 421 specific resource; i.e. we would never have a species with k=10 being outcompeted by a 422 423 species with k=5. In our model, the coexistence of species with larger differences than 424 expected at random is not related to possible intransitivity but specifically to stabilizing versatility in resources used. So, by using a model that isolates the role of niche differences, 425 we are able to support the idea that intransitivity emerging from multispecies competition 426 should not be pivotal for species coexistence in the absence of sufficient pairwise niche 427 differences (Godoy et al. 2017). 428

Finally, we must punctuate some limits of our approach. First, our model is an 429 interaction chain, where a species A has an indirect effect on species C by also competing 430 431 with the common competitor B. Another type of multispecies competition considers higher order interactions, where pairwise competition changes in the presence of a third competitor, 432 so that the impact of A on B is different when in pairwise or in triplets. The distinction 433 between interaction chains and higher-order interactions is determined by whether the 434 indirect effect emerges from a change in competitor density (interaction chain) or a change in 435 the per capita competitive effects (higher-order interaction). As we did not consider such 436

dynamics in our model, we cannot anticipate the impacts that these would have on the 437 patterns we found (see Levine et al. 2017). Second, in our study, we did not explicitly include 438 temporal or spatial variation mechanisms of coexistence. With more varying niche 439 dimensions, it is possible that local differences in resource use became less important and 440 thus local overdispersion may become weaker (Kraft et al. 2015). Third, our model is 441 strongly deterministic, not including neutral population dynamics that could modify 442 443 community patterns. Studies on these dynamics have shown that removing niche differences can have strong impacts on species coexistence. For example, D'Andrea and Ostling (2017) 444 445 found that neutral cases can even harbor larger number of coexisting species than niche based scenarios, especially if the number of available niches is limited. So, a way forward would be 446 to investigate how such dynamics would modify the patterns found here. 447

Concluding, here we introduced a new model of competition where species versatility 448 promotes niche differences. This model proved to be an interesting variation of the 449 MacArthur's consumer-resource model when species vary in their dependency for a 450 451 commonly exploited resource. Competition in nature is complex and should happen, not only in both ways, but also in many other ways. Besides this high complexity, we found that 452 overdispersion using nearest neighbor metrics was a recurrent pattern and thus could 453 454 signalize a master role that competition plays during community assembly. After some years of debate, our model and results highlight the role of species versatility and niche differences 455 and bring new perspectives for those aiming to infer the role of competition in molding 456 457 community patterns.

458

459 ACKNOWLEDGEMENTS

We are thankful to Raul Costa Pereira, Andros Gianuca, Franck Jabot, Ian Carroll, François
Massol, Matthew Leibold and Peter Chesson for comments that sharpened our ideas. We also

462	thank Annette Ostling, Nathan Kraft and an anonymous referee for comments and
463	discussions during the review process that greatly improved our manuscript. This study was
464	funded by grants #2013/50424-1, #2013/20540-0, #2014/24532-4 São Paulo Research
465	Foundation (FAPESP) and by grant 403723/2012-4, Conselho Nacional de Desenvolvimento
466	Científico e Tecnológico (CNPq). VSS thanks the Centre d'Ecologie et de Sciences de la
467	Conservation (CESCO) from the Muséum National d'Histoire Naturelle in Paris for kindly
468	receiving him during part of the elaboration of this manuscript.
469	
470	REFERENCES
471	Adler, P. B., A. Fajardo, A. R. Kleinhesselink and N. J. B. Kraft. 2013. Trait-based tests of
472	coexistence mechanisms. Ecology Letters 16:1294–1306.
473	Bellwood, D. R., P.C. Wainwright, C.J. Fulton and A.S. Hoey. 2006. Functional versatility
474	supports coral reef biodiversity. Proceedings of the Royal Society of London B:
475	Biological Sciences 273: 101-107.
476	Belmaker, J., C.H. Sekercioglu and W. Jetz. 2012. Global patterns of specialization and
477	coexistence in bird assemblages. Journal of Biogeography 39, 193-203.
478	Cadotte, M. W. and C. M. Tucker 2017. Should Environmental Filtering be Abandoned?
479	Trends in Ecology and Evolution 32: 429-437.
480	Chesson, P. 1991. A need for niches? Trends in Ecology and Evolution 6:26–8.
481	Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of
482	Ecology, Evolution and Systematics 31:343–358.
483	Chesson, P. 1990. MacArthur's consumer-resource model. Theoretical Population
484	Biology 37:26-38.
485	Chu, C. and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to
486	stabilize grassland coexistence. Ecological Monographs 85:373-392.

- 487 Devictor, V., R. Julliard and F. Jiguet. 2008. Distribution of specialist and generalist species
 488 along spatial gradients of habitat disturbance and fragmentation. Oikos 117: 507-514.
- 489 D'Andrea, R., and A. Ostling. 2016. Challenges in linking trait patterns to niche

differentiation. Oikos 125: 1369-1385.

- 491 D'Andrea, R., and A. Ostling. 2017. Biodiversity maintenance may be lower under partial
 492 niche differentiation than under neutrality. Ecology. Early view.
- Gallien, L. 2017. Intransitive competition and its effects on community functional diversity.
 Oikos 126: 615-623.
- 495 Gallien, L., N. E. Zimmermann, J. M. Levine and, P. B. Adler. 2017. The effects of

496 intransitive competition on coexistence. Ecology Letters 20: 791–800.

- Godoy, O., N. J. B. Kraft and J. M. Levine. 2014. Phylogenetic relatedness and the
 determinants of competitive outcomes. Ecology Letters 17:836–844.
- Godoy, O., D. B. Stouffer, N. J. Kraft and J. M. Levine. 2017. Intransitivity is infrequent and
 fails to promote annual plant coexistence without pairwise niche differences. Ecology
 98: 1193-1200.
- 502 Götzenberger, L., F. de Bello, K. A. Bråthen, J. Davison, A. Dubuis, A. Guisan et al. 2012.
- Ecological assembly rules in plant communities--approaches, patterns and prospects.
 Biological Reviews 87:111–27.
- Herben, T. and D. E. Goldberg. 2014. Community assembly by limiting similarity vs.
- competitive hierarchies: Testing the consequences of dispersion of individual traits.
 Journal of Ecology 102:156–166.
- 508 HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine and M. M. Mayfield. 2012.
- Rethinking Community Assembly through the Lens of Coexistence Theory. Annual
 Review of Ecology, Evolution and Systematics 43:227–248.
- 511 Kraft, N. J. B., W. K. Cornwell, C.O. Webb and D. D. Ackerly. 2007. Trait evolution,

- 512 community assembly, and the phylogenetic structure of ecological communities.
- 513 American Naturalist 170:271–83.
- 514 Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the
- multidimensional nature of species coexistence. Proceedings of the National Academy
 of Sciences 112:797–802.
- Lawlor, L. R. 1979. Direct and indirect effects of n-species competition. Oecologia 43:355364.
- Levine, S. H. 1976. Competitive interactions in ecosystems. American Naturalist 110:903910.
- Levine, J. M., J. Bascompte, P.B. Adler and S. Allesina. 2017. Beyond pairwise mechanisms
 of species coexistence in complex communities. Nature 546: 56-64.
- Liem, K. F. 1980. Adaptive significance of intra-and interspecific differences in the feeding
 repertoires of cichlid fishes. American zoologist 20: 295-314.
- Liem, K. F. 1990. Aquatic versus terrestrial feeding modes: possible impacts on the trophic
 ecology of vertebrates. American Zoologist 30: 209-221.
- 527 MacArthur, R. 1970. Species packing and competitive equilibrium for many
- 528 species. Theoretical Population Biology 1: 1-11.
- 529 MacArthur, R. H. and R. Levins. 1967. The Limiting Similarity, Convergence, and
- 530 Divergence of Coexisting Species. American Naturalist 101:377–385.
- 531 Mayfield, M. M. and J. M. Levine. 2010. Opposing effects of competitive exclusion on the
- 532 phylogenetic structure of communities. Ecology Letters 13:1085–93.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National
 Academy of Sciences 71:2141-2145.
- 535 Poff, N. L., M. A. Palmer, P. L. Angermeier, R. L. Vadas, C. C. Hakenkamp, A. Bely, P.
- 536 Arensburger, and A. P. Martin. 1993. Size structure of the metazoan community in a

- 537 Piedmont stream. Oecologia 95:202-209.
- Swenson, N. G. and B. J. Enquist. 2009. Opposing assembly mechanisms in a Neotropical
 dry forest: implications for phylogenetic and functional community ecology. Ecology
 90:2161–2170.
- 541 Tregonning, K. and A. Roberts. 1979. Complex systems which evolve towards homeostatis.
 542 Nature 281:563–564.
- 543 Warwick, R. M. and K. R. Clarke. 1984. Species size distributions in marine benthic
 544 communities. Oecologia 61:32-41.
- 545 Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an

546 example for rain forest trees. American Naturalist 156:145-155.

- 547 Weiher, E. and P. A. Keddy. 1995. Assembly Rules, Null Models, and Trait Dispersion: New
 548 Questions from Old Patterns. Oikos 74:159–164.
- 549 Wilson, W. G. and P. Lundberg. 2004. Biodiversity and the Lotka–Volterra theory of species

550 interactions: open systems and the distribution of logarithmic densities. Proceedings

- of the Royal Society of London B: Biological Sciences 271:1977-1984.
- 552
- 553
- 554
- 555
- 556
- 557
- 558
- 559

560

200

562 Figures legends

Figure 1. The differences between MacArthur's consumer-resource model and our new 563 model with ecological versatility. (A) In MacArthur's model, species have trait differences 564 that make their interactions less intense, given that competition happens for a linear array of 565 resources and each species is able to consume part of this array. (B) In nature, this would be 566 the case when, for example, birds have different beak sizes and each size enables the 567 568 consumption of a range of seed sizes. So, differences in beak sizes always decrease the interaction strength. (C) In our model, species also have traits that enable them to consume 569 570 part of the array of resources, but all species can consume one common resource. (D) This would be the case when all species of birds can eat a common seed or insect, but not all 571 species are dependent on these items. Some species have a more distinct beak morphology 572 573 that enables them to also eat other items. In this case, the interaction strength and thus niche overlap are determined by how much a species depends on this common resource. 574

575

Figure 2. Typical distributions used for k and θ parameters using beta distributions. The ks 576 relate to species fitness and θ s relate to species interaction strength. Using the simulated 577 species we calculated fitness-based distances between any two species *i* and *j* as $|\tilde{k}_i - \tilde{k}_j|$ and 578 579 niche-based distances as $1 - \theta_i \theta_i$. (a) A positive skewed distribution of ks with most species having low fitness. (b) A U-shaped distribution of ks with most species having low or high 580 fitness and few species having medium fitness. (c) A for bell-shaped distribution of ks with 581 most species having medium fitness. (d) A negative skewed distribution of ks with most 582 species having high fitness. (e) A negative skewed distribution of θ_i s resulting in most species 583 having low niche differences between them. (f) A bell-shaped distributions of θ_i s resulting in 584 most species having medium niche differences between them. (g) A uniform distribution of 585 586 θ_i s resulting in most of species having high niche differences between them.

588	Figure 3. Variation in species richness, Jaccard dissimilarity and species dispersion metrics
589	when simulating community assembly using different species pools. Blue boxplots are results
590	for species pools with average low niche differences, red boxplots for medium niche
591	differences and yellow for high niche differences. Within each color, the first boxplot is when
592	species have low fitness at the species pool scale, the second when species have medium
593	fitness values, the third when species have high fitness values and the forth when species
594	have a U-shaped distribution. We first applied indices SES-MNTD and SES-MPD separately
595	to niche distances and fitness distances between species and then to the overall functional
596	distances which combines niche and fitness as defined in the main text.
597	
598	Figure 4. Result of species dispersion metrics when species distance is calculated using
599	different weights for niche and fitness differences. Community assembly was performed
600	using a species pool with medium niche differences and medium fitness values at the species
601	pool scale.
602	
603	Figure 5. Results of richness, Jaccard dissimilarity and species dispersion metrics when we
604	varied the number of sequential colonization events during community assembly. Community
605	assembly was performed using a species pool with medium niche differences and fitness
606	values at the species pool scale. We first applied indices SES-MNTD and SES-MPD
607	separately to niche distances and fitness distances between species and then to the overall
608	functional distances which combines niche and fitness as defined in the main text.
609	
610	
611	

612 Figures

613 Figure 1.



 $\mathbf{\alpha}_{ij} = \mathbf{\Theta}_i \mathbf{\Theta}_j$

resources use (low θ).

Sp. 1

Sp. 3







- _ _ .





683 Figure 5.



697

698

699 Appendix S1 Manual to use functions of community assembly included in DataS1 700

701

707

702 ## Usage703

704 scenario_1_multispecies(a, t1, t2, f1, f2, nsim, tol=1e-8) 705 scenario_2_multispecies(a, t1, t2, f1, f2, nsim, tol=1e-8) 706 scenario_3_multispecies(nsim, t1, t2, f1, f2, tol=1e-8)

• a is the number of invasions (a numeric, integer);

nsim is the number of times the simulations are repeated: from the definition of the species
 pool to the calculation of the indices SES-MPD and SES-MNTD (a numeric, integer);

• t1, t2, f1, f2, are the parameters, bounded between 0 and 1, and used for beta distribution. t1 and t2 are respectively the α and β parameters of the beta distribution used for θ_i 's values. f1 and f2 are respectively the α and β parameters of the beta distribution used for \tilde{k}_i 's values. We considered various distributions for \tilde{k}_i 's and θ_i 's values as indicated in the main text.

tol is a tolerance threshold for null values: a value lower than tol is considered as null (a numeric)

717 718 Value

In function scenario_1_multispecies we varied the relative weight given to niche versus fitness traits in overall functional distances when calculating SES.MNTD and SES.MNTD (Figure 3 of the main text). In function scenario_2_multispecies we calculated all diversity indices for a fixed number of colonization events: richness; beta diversity; and SES.MNTD and SES.MNTD, applied to niche distances, fitness distances and overall functional distances with even weight given to niche versus fitness traits (Figure 2 of the main text). In function scenario 3 multispecies we also calculated all

725 diversity indices but varying the number of colonization events (Figure 4 of the main text).

All functions end up with a list. Each value of the list contains the result of a simulation, where simulation means that a pool of species has been obtained, 100 communities have been obtained by colonization from the species pool as described in the main text and metrics have been calculated on each community (species richness, beta diversity, and SES MNTD, SES MPD using niche traits, fitness or both) and averaged over the 100 communities. A simulation thus corresponds to a particular species pool.

All functions calculate all metrics (species richness, beta diversity, and SES MNTD, SES MPD using niche traits, fitness or both) except scenario_1_multispecies where only SES MNTD, SES MPD on

- both niche and fitness are calculated.
- When calculating averaged SES MNTD and averaged SES MPD over the 100 simulatedcommunities, communities, if any, with a single species were discarded.
- 737

738 Example of applications (to obtain similar figures as in the main text)

- 739 Comments are in bold letters following #.
- 740
- 741 ## Scenario 1
- 742

```
743
      # Example of application with a distribution beta(10, 5) for \theta_i's values and beta(2,2) for \tilde{k}_i's.
744
      This corresponds to bell-shaped distributions for interaction strength and for fitness.
745
      scenario 1 res 10 5 2 2 <- scenario 1 multispecies(a=100, 10,5,2,2,
746
      nsim=100)
747
748
      # The result of the first simulation scheme (from the definition of a unique species pool to the
749
      simulations of the 100 communities) can be obtained with the following instruction:
750
      scenario 1 res 10 5 2 2[[1]]
751
      $SES.MNTD
752
      niche1.fitness5 niche1.fitness4 niche1.fitness3 niche1.fitness2
753
            -1.0992815 -0.9177786 -0.6943723
                                                                   -0.1880420
754
      niche1.fitness1 niche2.fitness1 niche3.fitness1 niche4.fitness1
755
             0.4595798
                               0.8757695
                                                 1.0033666
                                                                   1.1138923
756
      niche5.fitness1
757
             1.2033374
758
759
      $SES.MPD
760
      niche1.fitness5 niche1.fitness4 niche1.fitness3 niche1.fitness2
761
            -2.0664446
                              -1.9937556
                                              -1.8735802
                                                                   -1.4928701
762
      niche1.fitness1 niche2.fitness1 niche3.fitness1 niche4.fitness1
763
            -0.7268908
                               0.2662877
                                                0.7062460
                                                                    0.9866080
764
      niche5.fitness1
765
             1.1153460
766
767
      # scenario 1 res 10 5 2 2[[1]] thus is a list of two vectors: the first one for metric MNTD, the
      second one for metric MPD. In each of the vector, the first value is the average metric value
768
      (either SES MNTD or SES MPD) over the 100 simulated communities when the fitness was
769
770
      given 5 times more weight than niche when calculating functional dissimilarities among
      species; the second value is the average metric value (either SES MNTD or SES MPD) over the
771
772
      100 simulated communities when the fitness was given 4 times more weight than niche when
773
      calculating functional dissimilarities among species, etc. "niche4.fitness1" thus for example
774
      means 4 times more weight to niche than to fitness.
775
776
      # scenario_1_res_10_5_2_2[[i]] and scenario_1_res_10_5_2_2[[j]] for any i different from j
      correspond to distinct species pools.
777
778
779
      # The following scripts led to Figure 4 of the main text
```

```
781
      scenario 1 SES.MNTD niche1.fitness5 <-</pre>
782
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
783
      x$SES.MNTD["niche1.fitness5"]))
784
      scenario 1 SES.MNTD niche1.fitness4 <-</pre>
785
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
786
      x$SES.MNTD["niche1.fitness4"]))
787
      scenario 1 SES.MNTD niche1.fitness3 <-</pre>
788
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
789
      x$SES.MNTD["niche1.fitness3"]))
790
      scenario 1 SES.MNTD niche1.fitness2 <-</pre>
791
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
792
      x$SES.MNTD["niche1.fitness2"]))
793
      scenario 1 SES.MNTD niche1.fitness1 <-</pre>
794
      unlist(lapply(scenario_1_res_10_5_2_2, function(x)
795
      x$SES.MNTD["niche1.fitness1"]))
```

```
796
      scenario 1 SES.MNTD niche2.fitness1 <-</pre>
797
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
798
      x$SES.MNTD["niche2.fitness1"]))
799
      scenario 1 SES.MNTD niche3.fitness1 <-</pre>
800
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
801
      x$SES.MNTD["niche3.fitness1"]))
802
      scenario 1 SES.MNTD niche4.fitness1 <-</pre>
803
      unlist(lapply(scenario_1_res_10_5_2_2, function(x)
804
      x$SES.MNTD["niche4.fitness1"]))
805
      scenario 1 SES.MNTD niche5.fitness1 <-</pre>
806
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
807
      x$SES.MNTD["niche5.fitness1"]))
808
809
      scenario 1 MNTD <- list(scenario 1 SES.MNTD nichel.fitness5,</pre>
810
      scenario 1 SES.MNTD nichel.fitness4, scenario 1 SES.MNTD nichel.fitness3,
811
      scenario 1 SES.MNTD nichel.fitness2, scenario 1 SES.MNTD nichel.fitness1,
812
      scenario 1 SES.MNTD niche2.fitness1, scenario 1 SES.MNTD niche3.fitness1,
813
      scenario 1 SES.MNTD niche4.fitness1, scenario 1 SES.MNTD niche5.fitness1)
814
815
816
      scenario 1 SES.MPD niche1.fitness5 <-</pre>
817
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
818
      x$SES.MPD["niche1.fitness5"]))
819
      scenario 1 SES.MPD niche1.fitness4 <-</pre>
820
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
821
      x$SES.MPD["niche1.fitness4"]))
822
      scenario 1 SES.MPD niche1.fitness3 <-</pre>
823
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
824
      x$SES.MPD["niche1.fitness3"]))
825
      scenario 1 SES.MPD niche1.fitness2 <-</pre>
826
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
      x$SES.MPD["niche1.fitness2"]))
827
828
      scenario 1 SES.MPD niche1.fitness1 <-</pre>
829
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
830
      x$SES.MPD["niche1.fitness1"]))
831
      scenario 1 SES.MPD niche2.fitness1 <-</pre>
832
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
833
      x$SES.MPD["niche2.fitness1"]))
834
      scenario 1 SES.MPD niche3.fitness1 <-</pre>
835
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
836
      x$SES.MPD["niche3.fitness1"]))
837
      scenario 1 SES.MPD niche4.fitness1 <-</pre>
838
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
839
      x$SES.MPD["niche4.fitness1"]))
840
      scenario 1 SES.MPD niche5.fitness1 <-</pre>
841
      unlist(lapply(scenario 1 res 10 5 2 2, function(x)
842
      x$SES.MPD["niche5.fitness1"]))
843
844
      scenario 1 MPD <- list(scenario 1 SES.MPD niche1.fitness5,</pre>
      scenario_1_SES.MPD_niche1.fitness4, scenario 1 SES.MPD niche1.fitness3,
845
      scenario 1 SES.MPD nichel.fitness2, scenario 1 SES.MPD nichel.fitness1,
846
847
      scenario 1 SES.MPD niche2.fitness1, scenario 1 SES.MPD niche3.fitness1,
848
      scenario 1 SES.MPD niche4.fitness1, scenario 1 SES.MPD niche5.fitness1)
```

```
849
850
      par(mfrow=c(2,1))
      boxplot(scenario 1 MNTD, ylim=c(-8,8), ylab="SES.MNTD", xlab="Nb of
851
852
      fitness:niche traits",
      names=c("5:1","4:1","3:1","2:1","1:1","1:2","1:3","1:4","1:5"))
853
854
      abline(h=0)
855
856
      boxplot(scenario 1 MPD, ylim=c(-8,8), ylab="SES.MPD", xlab="Nb of
857
      fitness:niche traits",
      names=c("5:1","4:1","3:1","2:1","1:1","1:2","1:3","1:4","1:5"))
858
859
      abline(h=0)
860
```



```
861
```

Duplication of Figure 4 of the main text. Result of species dispersion metrics when species
distance is calculated using different weights for niche and fitness differences. Community
assembly was performed using a species pool with medium niche differences and medium
fitness values at the species pool scale.

868 <u>## Scenario 2</u>

869 870 # We considered 3 sets of parameters for the beta distributions of the θ_i 's values and and 4 for 871 the beta distributions of the \tilde{k}_i 's as specified in the main text. 872 873 scenario_2_res_10_1_1_5 <- scenario_2_multispecies(a=100, 10,1,1,5,

```
874 nsim=100)
```

```
875
      scenario 2 res 10 1 05 05 <- scenario 2 multispecies(a=100, 10,1,0.5,0.5,
876
      nsim=100)
877
      scenario 2 res 10 1 2 2 <- scenario 2 multispecies(a=100, 10,1,2,2,
878
      nsim=100)
879
      scenario 2 res 10 1 5 1 <- scenario 2 multispecies(a=100, 10,1,5,1,
880
      nsim=100)
881
882
883
      scenario 2 res 10 5 1 5 <- scenario 2 multispecies(a=100, 10,5,1,5,
884
      nsim=100)
      scenario 2 res 10 5 05 05 <- scenario 2 multispecies (a=100, 10,5,0.5,0.5,
885
886
      nsim=100)
887
      scenario 2 res 10 5 2 2 <- scenario 2 multispecies(a=100, 10,5,2,2,
888
      nsim=100)
889
      scenario 2 res 10 5 5 1 <- scenario 2 multispecies (a=100, 10,5,5,1,
890
      nsim=100)
891
892
      scenario 2 res 1 1 1 5 <- scenario 2 multispecies (a=100, 1,1,1,5,
893
      nsim=100)
894
      scenario 2 res 1 1 05 05 <- scenario 2 multispecies(a=100, 1,1,0.5,0.5,
895
      nsim=100)
      scenario 2 res 1 1 2 2 <- scenario 2 multispecies(a=100, 1,1,2,2,
896
897
      nsim=100)
898
      scenario 2 res 1 1 5 1 <- scenario 2 multispecies(a=100, 1,1,5,1,</pre>
899
      nsim=100)
900
      # For example, with a distribution beta(10, 5) for \theta_i's values and beta(2,2) for \tilde{k}_i's, the result of
901
902
      the first simulation schemes (from the definition of a unique species pool to the simulations of
      the 100 communities, with 100% of niche range) can be obtained with the following
903
904
      instruction:
905
906
      scenario 2 res 10 5 2 2[[1]]
907
            richness
                                beta SES.MNTDniche SES.MPDniche SES.MNTDfitness
           13.2400000
908
                           0.5992819
                                          2.2651896
                                                           2.7483701 -1.3339585
909
       SES.MPDfitness SES.MNTDoverall SES.MPDoverall
910
           -1.9873402
                           2.4475813
                                           0.5512119
911
912
      # scenario_2_res_10_5_2_2[[1]] is thus a vector of eight values: the first gives the average
      richness in the 100 simulated communities, the second one the average beta diversity among
913
914
      the 100 communities (pairwise Jaccard dissimilarity), then the other values provide indices
915
      SES MNTD and SES MPD as specified calculated with the niche trait, the fitness or both. For
      example, "SES.MPDoverall" gives the SES MPD value applied to both niche and fitness and
916
      averaged over the 100 simulated communities, while "SES.MNTDniche" gives the SES MNTD
```

- averaged over the 100 simulated communities, while "SES.MNTDniche" gives
 value applied to niche only and averaged over the 100 simulated communities.
- 919
- 920 # scenario_2_res_10_5_2_2 [[i]] and scenario_2_res_10_5_2_2 [[j]] for any i different from j 921 correspond to distinct species pools.

```
922
923 # The following scripts led to Figure 3 of the main text
924
925 vecD =c("10_1_1_5", "10_1_05_05", "10_1_2_2", "10_1_5_1",
926 "10_5_1_5", "10_5_05_05", "10_5_2_2", "10_5_5_1",
927 "1_1_1_5", "1_1_05_05", "1_1_2_2", "1_1_5_1")
```

```
928
929
     scenario 2 res <- list(</pre>
930
     scenario 2 res 10 1 1 5, scenario 2 res 10 1 05 05,
931
     scenario 2 res 10 1 2 2, scenario 2 res 10 1 5 1,
932
     scenario 2 res 10 5 1 5, scenario 2 res 10 5 05,
933
     scenario 2 res 10 5 2 2, scenario 2 res 10 5 5 1,
934
     scenario 2 res 1 1 1 5, scenario 2 res 1 1 05 05, scenario 2 res 1 1 2 2,
935
     scenario 2 res 1 1 5 1)
936
937
     scenario 2 MNTDniche <- lapply(scenario 2 res, function(v)</pre>
938
     as.vector(unlist(lapply(v, function(x) x["SES.MNTDniche"]))))
939
940
     scenario 2 MNTDfitness <- lapply(scenario 2 res, function(v)</pre>
941
     as.vector(unlist(lapply(v, function(x) x["SES.MNTDfitness"]))))
942
943
     scenario 2 MNTDoverall <- lapply(scenario 2 res, function(v)</pre>
944
     as.vector(unlist(lapply(v, function(x) x["SES.MNTDoverall"]))))
945
     scenario 2 MPDniche <- lapply(scenario_2_res, function(v)</pre>
946
947
     as.vector(unlist(lapply(v, function(x) x["SES.MPDniche"]))))
948
949
     scenario 2 MPDfitness <- lapply(scenario 2 res, function(v)</pre>
950
     as.vector(unlist(lapply(v, function(x) x["SES.MPDfitness"]))))
951
952
     scenario 2 MPDoverall <- lapply(scenario 2 res, function(v)
953
     as.vector(unlist(lapply(v, function(x) x["SES.MPDoverall"]))))
954
     scenario 2 richness <- lapply(scenario 2 res, function(v)</pre>
955
     as.vector(unlist(lapply(v, function(x) x["richness"]))))
956
957
958
     scenario 2 beta <- lapply(scenario 2 res, function(v)</pre>
959
     as.vector(unlist(lapply(v, function(x) x["beta"]))))
960
961
     par(mfrow=c(2,4))
962
     boxplot(scenario 2 richness, ylim=c(0,100), names=vecD, las=3,
963
     ylab="Richness", col=c(rep("blue", 4), rep("red", 4), rep("yellow", 4)))
964
     boxplot(scenario 2 beta, ylim=c(0,1), names=vecD, las=3, ylab="Beta
     diversity", col=c(rep("blue", 4), rep("red", 4), rep("yellow", 4)))
965
966
     boxplot(scenario 2 MNTDniche, ylim=c(-10,10), names=vecD, las=3,
967
     ylab="SES.MNTD niche distance", col=c(rep("blue", 4), rep("red", 4),
968
     rep("yellow", 4)))
969
     abline(h=0)
970
     boxplot(scenario 2 MPDniche, ylim=c(-10,10), names=vecD, las=3,
     ylab="SES.MPD niche distance", col=c(rep("blue", 4), rep("red", 4),
971
972
     rep("yellow", 4)))
973
     abline(h=0)
974
     boxplot(scenario 2 MNTDfitness, ylim=c(-10,10), names=vecD, las=3,
975
     ylab="SES.MNTD fitness distance", col=c(rep("blue", 4), rep("red", 4),
976
     rep("yellow", 4)))
977
     abline(h=0)
978
     boxplot(scenario 2 MPDfitness, ylim=c(-10,10), names=vecD, las=3,
979
     ylab="SES.MPD fitness distance", col=c(rep("blue", 4), rep("red", 4),
980
     rep("yellow", 4)))
```

```
981 abline(h=0)
```

```
982
     boxplot(scenario 2 MNTDoverall, ylim=c(-10,10), names=vecD, las=3,
983
     vlab="SES.MNTD overall distance", col=c(rep("blue", 4), rep("red",
                                                                         4),
984
      rep("yellow", 4)))
     abline(h=0)
985
986
     boxplot(scenario 2 MPDoverall, ylim=c(-10,10), names=vecD, las=3,
     ylab="SES.MPD overall distance", col=c(rep("blue", 4), rep("red", 4),
987
988
      rep("yellow", 4)))
989
     abline(h=0)
990
```



Duplication of Figure 3 of the main text. Variation in species richness, Jaccard dissimilarity 992 993 and species dispersion metrics when simulating community assembly using different species pools. Blue boxplots are results for species pools with average low niche differences, red 994 995 boxplots for medium niche differences and yellow for high niche differences. Within each color, the first boxplot is when species have low fitness at the species pool scale, the second 996 when species have medium fitness values, the third when species have high fitness values and 997 the forth when species have a U-shaped distribution. We first applied indices SES-MNTD 998 999 and SES-MPD separately to niche distances and fitness distances between species and then to 1000 the overall functional distances which combines niche and fitness as defined in the main text. 1001 Legend:

- 1002 Blue= Niche differences are high
- 1003 Red=Niche differences are medium
- 1004 Yellow=Niche differences are low

For a given color, left=positive skewed fitness values (most species have low fitness, a few species have high fitness); middle left=U shaped distributed fitness values (many low and high fitness, less medium fitness values); middle left=Bell-shaped distributed fitness values (many medium fitness values); right=negative skewed fitness values (most species have high fitness, a few species have low fitness); ## Scenario 3 # Example of application with a distribution beta(10, 5) for θ_i 's values and beta(2,2) for \tilde{k}_i 's. This corresponds to bell-shaped distributions for interaction strength and for fitness. scenario 3 res 10 5 2 2 <- scenario 3 multispecies(nsim=100, 10,5,2,2) # The result of the first simulation can be obtained with the following instruction: scenario 3 res 10 5 2 2[[1]] \$richness 100 300 500 4.46 10.43 12.87 14.74 14.91 \$beta 0.95226597 0.77407196 0.57021583 0.11711865 0.02511381 \$SES.MNTDniche

1029105010030050010300.33965791.46325822.49611323.85620993.67113811031

\$SES.MNTDfitness -1.007009 -1.894202 -2.162191 -2.399947 -2.419053 \$SES.MPDfitness

 1042
 -1.289755
 -2.456777
 -2.815547
 -3.365079
 -3.337911

 1043
 \$SES.MNTDoverall

 1045
 10
 50
 100
 300

 -0.4096832 0.9330254 1.9980024 2.7822315 2.6177442 **1048** \$SES.MPDoverall **1049** 10 50 100 300 500 **1050** -0.7978737 -0.8030256 -0.4172586 -0.4110750 -0.5757312

scenario_3_res_10_5_2_2[[1]] is thus a list of eight vectors: the first gives the average richness in the 100 simulated communities, the second one the average beta diversity among the 100 communities (pairwise Jaccard dissimilarity), then the other vectors provide indices SES MNTD and SES MPD as specified calculated with the niche trait, the fitness or both. For

1056 example, \$SES.MPDoverall gives the SES MPD value applied to both niche and fitness and averaged over the 100 simulated communities, while \$SES.MNTDniche gives the SES MNTD 1057 value applied to niche only and averaged over the 100 simulated communities. The names 1058 1059 attributed above each value of a vector indicate the numbers of colonization events used in 1060 the model. 1061 1062 # scenario_3_res_10_5_2_2 [[i]] and scenario_3_res_10_5_2_2 [[j]] for any i different from j 1063 correspond to distinct species pools. 1064 1065 # The following scripts led to Figure 5 of the main text 1066 1067 vecC = as.character(c(10, 50, 100, 300, 500))1068 scenario 3 MNTDniche 10 5 2 2 <- lapply(vecC, function(v)</pre> 1069 1070 unlist(lapply(scenario 3 res 10 5 2 2, function(x) 1071 x\$SES.MNTDniche[v]))) 1072 scenario_3_MNTDfitness_10_5_2_2 <- lapply(vecC, function(v)</pre> 1073 1074 unlist(lapply(scenario 3 res 10 5 2 2, function(x) 1075 x\$SES.MNTDfitness[v])) 1076 scenario 3 MNTDoverall 10 5 2 2 <- lapply(vecC, function(v)</pre> 1077 1078 unlist(lapply(scenario 3 res 10 5 2 2, function(x) 1079 x\$SES.MNTDoverall[v]))) 1080 1081 scenario 3 MPDniche 10 5 2 2 <- lapply(vecC, function(v)</pre> unlist(lapply(scenario_3_res_10 5 2 2, function(x) 1082 1083 x\$SES.MPDniche[v]))) 1084 1085 scenario 3 MPDfitness 10 5 2 2 <- lapply(vecC, function(v)</pre> unlist(lapply(scenario 3 res 10 5 2 2, function(x) 1086 1087 x\$SES.MPDfitness[v]))) 1088 1089 scenario 3 MPDoverall 10 5 2 2 <- lapply(vecC, function(v)</pre> 1090 unlist (lapply (scenario 3 res 10 5 2 2, function (x) 1091 x\$SES.MPDoverall[v]))) 1092 scenario 3 richness 10 5 2 2 <- lapply(vecC, function(v)</pre> 1093 unlist(lapply(scenario 3 res 10 5 2 2, function(x) x\$richness[v]))) 1094 1095 1096 scenario_3_beta_10_5_2_2 <- lapply(vecC, function(v)</pre> 1097 unlist(lapply(scenario 3 res 10 5 2 2, function(x) x\$beta[v]))) 1098 1099 1100 1101 par(mfrow=c(2, 4))boxplot(scenario 3 richness 10 5 2 2, ylim=c(0,100), names=vecC, 1102 1103 las=3, xlab="Colonization intensity", ylab="Richness") boxplot(scenario 3 beta 10 5 2 2, ylim=c(0,1), names=vecC, las=3, 1104 1105 xlab="Colonization intensity", ylab="Beta diversity") 1106 boxplot(scenario 3 MNTDniche 10 5 2 2, ylim=c(-9,9), names=vecC, 1107 las=3, xlab="Colonization intensity", ylab="SES.MNTD niche distance") 1108 abline(h=0) boxplot(scenario_3_MPDniche_10_5_2_2, ylim=c(-9,9), names=vecC, las=3, 1109 1110 xlab="Colonization intensity", ylab="SES.MPD niche distance")

```
1111
      abline(h=0)
      boxplot(scenario 3 MNTDfitness 10 5 2 2, ylim=c(-9,9), names=vecC,
1112
      las=3, xlab="Colonization intensity", ylab="SES.MNTD fitness distance")
1113
1114
      abline(h=0)
      boxplot(scenario 3 MPDfitness 10 5 2 2, ylim=c(-9,9), names=vecC,
1115
1116
      las=3, xlab="Colonization intensity", ylab="SES.MPD fitness distance")
1117
      abline(h=0)
      boxplot(scenario 3 MNTDoverall 10 5 2 2, ylim=c(-9,9), names=vecC,
1118
      las=3, xlab="Colonization intensity", ylab="SES.MNTD overall distance")
1119
      abline(h=0)
1120
1121
      boxplot(scenario 3 MPDoverall 10 5 2 2, ylim=c(-9,9), names=vecC,
      las=3, xlab="Colonization intensity", ylab="SES.MPD overall distance")
1122
1123
      abline(h=0)
1124
```



Duplication of figure 5 of the main text. Results of richness, Jaccard dissimilarity and
species dispersion metrics when we varied the number of sequential colonization events
during community assembly. Community assembly was performed using a species pool with
medium niche differences and fitness values at the species pool scale. We first applied
indices SES-MNTD and SES-MPD separately to niche distances and fitness distances
between species and then to the overall functional distances which combines niche and
fitness as defined in the main text.

- 1134
- 1135
- 1136

1138

- 1139
- 1140
- 1141

1142 Appendix S2 Deriving an equalizing/stabilizing additive decomposition in a multi-1143 species competition model starting with consumer-resource model (MacArthur 1970)

1144 In this appendix, we first provide the detailed demonstration of the method used in the 1145 main text. Second, we justify the form of the interaction coefficients which is considered 1146 in the model by relating it with a general resource competition model.

1147 Deriving the low-density long term growth rate and its stabilizing and equalizing 1148 components in a multispecies competition model with interaction coefficients such as 1149 $\alpha_{ii} = \theta_i \theta_i$

For our study, we searched a reference model that respects Chesson's (2000) following approximation to the long-term low-density growth rate (equation 4 in Chesson 2000):

1152
$$\overline{r_i} \approx b_i \left(k_i - \frac{\sum_{s \neq i} k_s}{n-1}\right) + b_i \frac{(1-\rho)}{n-1}D$$

where *n* is the number of species in the system, the *ks* are measures of fitness of individual species, $(\sum_{s\neq i} k_s)/(n-1)$ is the average fitness of the competitors of *i*, ρ is a measure of niche overlap, and *D* is a positive constant. This equation is composed of an equalizing term

$$b_i\left(k_i-\frac{\sum_{s\neq i}k_s}{n-1}\right)$$

1156 and a stabilizing term

- 1157 $b_i \frac{(1-\rho)}{n-1} D.$
- 1158

1159 We started from the resource consumption model (equations 1 and 2 in Chesson 1990):

1160
$$\begin{cases} \frac{1}{X_{i}} \frac{dX_{i}}{dt} = b_{i} [\sum_{l=1}^{m} c_{il} w_{l} R_{l} - m_{i}] \\ \frac{1}{R_{l}} \frac{dR_{l}}{dt} = r_{l} \left(1 - \frac{R_{l}}{K_{l}} \right) - \sum_{i=1}^{n} c_{il} X_{i} \end{cases}$$
(Eq. 1161 S1)

- 1162 where *i* is a consumer species; X_i is population density; R_l is the density of food resource *l*; w_l
- 1163 is the value of one unit of resource l to the consumer; c_{il} is the rate at which consumer
- species *i* captures resource *I* per unit abundance of resource *I*; m_i is the total value of
- resource that must be harvested per capita for the growth rate to be exactly 0; b_i is a factor
- 1166 converting the resource excess into the per capita growth rate; r_l is the growth rate and K_l the
- 1167 carrying capacity for resource l.

Assuming a separation of time scales between resource and consumer dynamics, one obtainsthe quasi-static equilibrium of resources:

1170
$$R_{l}(t) = \left[1 - \frac{1}{r_{l}} \sum_{i=1}^{n} c_{il} X_{i}(t)\right] K_{l}$$
(Eq. 1171 S2)

1172 Introducing (Eq. S2) in the consumer dynamics presented in (Eq. S1) yields:

1173
$$\frac{1}{X_i} \frac{dX_i}{dt} = b_i \left[\sum_{l=1}^m c_{il} w_l K_l - m_i - \sum_{l=1}^m \sum_{j=1}^n c_{jl} c_{il} \frac{w_l K_l}{r_l} X_j \right]$$
(Eq. S3)

(Eq. S3) can be written using vectors (in bold letters) and matrices (in bold capital letters) asfollows:

1176
$$\frac{1}{X_i} \frac{dX_i}{dt} = b_i \left[\left[{}^{t} \boldsymbol{r} \boldsymbol{M} \boldsymbol{c}_i - m_i - \| \boldsymbol{c}_i \|_{\boldsymbol{M}} \sum_{j=1}^{n} \frac{{}^{t} \boldsymbol{c}_j \boldsymbol{M} \boldsymbol{c}_i}{\| \boldsymbol{c}_i \|_{\boldsymbol{M}} \| \boldsymbol{c}_j \|_{\boldsymbol{M}}} \| \boldsymbol{c}_j \|_{\boldsymbol{M}} X_j \right]$$
(Eq. S4)

1177 where \boldsymbol{M} is a diagonal matrix such as $M_{ll} = \frac{w_l K_l}{r_l}$ and $\|.\|_{\boldsymbol{M}}$ is the corresponding Euclidean 1178 norm. Then, we can define the "standardized density" $\tilde{X}_i = \|\boldsymbol{c}_i\|_M X_i$ so that (Eq. S4) yields:

1179
$$\frac{1}{\tilde{X}_i} \frac{d\tilde{X}_i}{dt} = \tilde{b}_i \left[\tilde{K}_i - \sum_{j=1}^n \tilde{\alpha}_{ij} \tilde{X}_j \right]$$
(Eq. 1180 S5)

1181 where we have defined the standardized parameters:

$$\tilde{b}_i = \|\boldsymbol{c}_i\|_M b_i$$

1183
$$\tilde{k}_{i} = \frac{{}^{t} r_{M} c_{i} - m_{i}}{\|c_{i}\|_{M}} = \left[\frac{{}^{t} r_{M} c_{i}}{\|c_{i}\|_{M} \|r\|_{M}}\right] \|r\|_{M} - \frac{m_{i}}{\|c_{i}\|_{M}}$$

1184
$$\widetilde{\alpha}_{ij} = \frac{{}^{t}c_{j}Mc_{i}}{\left\|c_{i}\right\|_{M}\left\|c_{j}\right\|_{M}}$$

1185 Importantly, $\tilde{\alpha}_{ii} = 1$ and the Cauchy-Schwartz inequality ensures that $\tilde{\alpha}_{ij} < 1$ when $i \neq j$. 1186 Consider species *i* at low density, and assume that the n - 1 other species can coexist. Then 1187 all the other species $j \neq i$ harboring their equilibrium density \tilde{X}_{ji} (second subscript "*i*" 1188 meaning "in the absence of species *i*"). Then the long-term growth rate at low density of 1189 species *i*, \bar{r}_i , is obtained by neglecting \tilde{X}_i and setting the \tilde{X}_j s to \tilde{X}_{ji} s in (Eq. S5):

1190
$$\bar{r}_i = \tilde{b}_i \left[\tilde{k}_i - \sum_{\substack{j=1\\j\neq i}}^n \tilde{\alpha}_{ij} \tilde{X}_{ji} \right]$$
(Eq. 1191 S6)

1192 Note that this is reminiscent of equation (58) of Chesson (1994), but in a standardized 1193 formulation of the system. 1194 We now consider n > 2 species in competition. We define \tilde{A} the matrix of standardized 1195 interaction coefficients among species ($\tilde{A}_{ij} = \tilde{\alpha}_{ij}$). Then for any pair of species $i \neq j$, taking 1196 the equilibrium of *j* in the n - 1 species system where *i* is absent in equation (Eq. S5) yields:

1197
$$\widetilde{A}\widetilde{X} = \widetilde{K} + \Delta$$
 (Eq. S7)

1198 where we use the convention that $\tilde{X}_{ii} = 0$, we define $\tilde{K}_{ij} = \tilde{k}_i$ and Δ a diagonal matrix with 1199 unknown coefficients. (Eq. S7) implies that:

1200
$$\widetilde{X} = \widetilde{A}^{-1} (\widetilde{K} + \Delta)$$
 (Eq.
1201 S8)

1202 Without making any assumptions on the coefficients of \tilde{A} , combining (Eq. S6) and (Eq. S7) 1203 yields:

1204
$$\bar{r}_i = -\tilde{b}_i \Delta_{ii}$$
 (Eq. 1205 S9)

1206 Δ_{ii} can be computed by considering the (i, i) coefficient in (Eq. S8) and using that $\tilde{X}_{ii} = 0$:

1207
$$[\Delta]_{ii} = -\frac{[\tilde{A}^{-1}\tilde{K}]_{ii}}{[\tilde{A}^{-1}]_{ii}}$$
 (Eq.

- 1208 S10)
- 1209 Using (Eq. S10) in (Eq. S9) yields:

1210
$$\bar{r}_i = \tilde{b}_i \frac{\left[\tilde{A}^{-1}\tilde{K}\right]_{ii}}{\left[\tilde{A}^{-1}\right]_{ii}} = \tilde{b}_i \left(\tilde{k}_i + \sum_{\substack{j=1\\j\neq i}}^n \frac{\left[\tilde{A}^{-1}\right]_{ij}}{\left[\tilde{A}^{-1}\right]_{ii}}\tilde{k}_j\right)$$
(Eq. S11)

1211 We now consider a broader class of interaction matrices with the following form:

1212
$$\widetilde{A} = \boldsymbol{\theta}^{t} \boldsymbol{\theta} + \boldsymbol{D}$$
 (Eq. 1213 S12)

1214 where:

1215 -
$$\boldsymbol{\theta} = (\theta_1, \theta_2, ..., \theta_n)$$
 is a vector of positive real numbers such as for all $i, \theta_i < 1$;
1216 - \boldsymbol{D} is a diagonal matrix such as $D_{ii} = 1 - \theta_i^2$ for all i .

1217 (Eq. S12) implies that $\alpha_{ij} = \theta_i \theta_j < 1$ for all $i \neq j$. We develop in the next section how such 1218 interaction matrices naturally emerge from competition for resources among species.

1219 If \widetilde{A} verifies (Eq. S12) then:

1220
$$\widetilde{A}^{-1} = \left[I - \frac{D^{-1}\theta^{-t}\theta}{1 + \|\theta\|_{D^{-1}}^2}\right]D^{-1}$$
 (Eq. 1221 S13)

1222 Using (Eq. S13) in (Eq. S11) yields:

$$1223 \quad \bar{r}_{i} = \tilde{b}_{i} \left(\tilde{k}_{i} - \sum_{\substack{j=1\\j\neq i}}^{n} \frac{\frac{\theta_{i}\theta_{j}[\boldsymbol{p}^{-1}]_{jj}}{1 + \|\boldsymbol{\theta}\|_{\boldsymbol{p}^{-1}}^{2}}}{\left(1 - \frac{|\boldsymbol{p}^{-1}]_{ii}\theta_{i}^{2}}{1 + \|\boldsymbol{\theta}\|_{\boldsymbol{p}^{-1}}^{2}}\right)} \tilde{k}_{j} \right)$$

$$1224 \quad = \tilde{b}_{i} \left(\tilde{k}_{i} - \frac{\theta_{i}}{\left(1 + \|\boldsymbol{\theta}\|_{\boldsymbol{p}^{-1}}^{2} - \frac{\theta_{i}^{2}}{1 - \theta_{i}^{2}}\right)} \sum_{\substack{j=1\\j\neq i}}^{n} \frac{\theta_{j}}{1 - \theta_{j}^{2}} \tilde{k}_{j} \right)$$

1225
$$= \tilde{b}_i \left(\tilde{k}_i - \frac{\theta_i}{\left(1 + \sum_{\substack{l=1\\l \neq i}}^n \frac{\theta_l^2}{1 - \theta_l^2}\right)} \sum_{\substack{j=1\\j \neq i}}^n \frac{\theta_j}{1 - \theta_j^2} \tilde{k}_j \right)$$
(Eq. S14)

We now seek to decompose equation (Eq. S14) in stabilizing and equalizing terms as in Chesson's (2000) framework. To find the stabilizing term, we first looked at the long-term growth rate at low density when all the species have the same fitness \tilde{k} . In this case, only the stabilizing should act on coexistence. When all the fitnesses are equal, (Eq. S14) becomes:

1230
$$\bar{r}_{i} = \tilde{b}_{i}\tilde{k} \left(1 - \frac{\theta_{i}\sum_{\substack{j=1\\j\neq i}}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}}}{1 + \sum_{\substack{l=1\\l\neq i}}^{n} \frac{\theta_{l}^{2}}{1-\theta_{l}^{2}}} \right)$$
(Eq. S15)

We now search for the corresponding equalizing term in an additive decomposition as in Chesson's (2000) framework (Eq. 1 above). Starting from (Eq. S14), we obtained the following final expression for the long-term growth rate of a species:

$$1234 \qquad \bar{r}_{i} = \tilde{b}_{i} \left(\tilde{k}_{i} - \frac{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}} \tilde{k}_{j}}{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}}} + \frac{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}} \tilde{k}_{j}}{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}}} \left(1 - \frac{\sum_{j=1}^{n} \frac{\theta_{i}\theta_{j}}{1-\theta_{j}^{2}}}{1 + \sum_{l=1}^{n} \frac{\theta_{l}}{1-\theta_{l}^{2}}} \right) \right) = \tilde{b}_{i} \left(\tilde{k}_{i} - \bar{k}_{i} + (1 - \rho_{i}) \bar{k}_{i} \right) \qquad (Eq. S16)$$

1235 where

1236
$$\overline{k}_{i} = \frac{\sum_{j=1}^{n} \frac{0_{j}}{1-\theta_{j}^{2}} \widetilde{k}}{\sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}}}$$

1237
$$\rho_{i} = \frac{\frac{\theta_{i} \sum_{j=1}^{n} \frac{\theta_{j}}{1-\theta_{j}^{2}}}{\frac{j \neq i}{1-\theta_{j}^{2}}}}{\frac{\theta_{i}^{2}}{1+\sum_{j=1}^{n} \frac{\theta_{j}^{2}}{1-\theta_{j}^{2}}}}$$

1238 We thus retrieve in (Eq. S16) a stabilizing term with a form consistent with Chesson (2000; 1239 equation (4)). Note that changing θ_i affects ρ_i but not \bar{k}_i , which is a desirable property of the 1240 equalizing/stabilizing decomposition. The main difference with Chesson's (2000) framework 1241 is that the \bar{k}_i is not a simple arithmetic mean of the fitnesses but also has to include some 1242 interaction effects of other species. Changing interactions among species thus changes the \bar{k}_i s 1243 even of fitnesses are maintained constant. 1244 <u>Making explicit the resource competition model underpinning the choice $\alpha_{ij} = \theta_i \theta_j$ </u>

1245 We note $c_i = (c_{i1}, ..., c_{il})$

1246 In any resource competition multispecies model, c_i , the consumption vectors of species *i* can 1247 be written as follows:

$$c_i = c + u_i \tag{Eq. S17}$$

1249 Where c is a component of the consumption vector which is shared among all the species and 1250 u_i is a component of the consumption vector which is specific to species *i*. (Eq. S17) implies 1251 that the interaction coefficients verify:

1252
$$\widetilde{\alpha}_{ij} = \frac{{}^{t}c_{j}Mc_{i}}{\|c_{i}\|_{M}\|c_{j}\|_{M}} = \frac{{}^{t}c_{M}c_{+} {}^{t}u_{i}Mc_{+} {}^{t}u_{j}Mc_{+} {}^{t}u_{i}Mu_{j}}{\|c_{i}\|_{M}\|c_{j}\|_{M}}$$
(Eq. 1253 S18)

1254 (Eq. S18) implies that choosing the u_i s such as:

1255 for all
$$i$$
, ${}^{t}\boldsymbol{u}_{i}M\boldsymbol{c} = 0$ (Eq.

1256 S19a)

1257 for all
$$i \neq j$$
, ${}^{t}\boldsymbol{u}_{i}M\boldsymbol{u}_{j} = 0$ (Eq.
1258 S19b)

1259 yields:

1260
$$\tilde{\alpha}_{ij} = \frac{\|\boldsymbol{c}\|_M^2}{\|\boldsymbol{c}_i\|_M \|\boldsymbol{c}_j\|_M} = \theta_i \theta_j$$
(Eq. S20)

1261 where $\theta_i = \frac{\|c\|_M}{\|c_i\|_M} = \frac{\|c\|_M}{\sqrt{\|c\|_M^2 + \|u_i\|_M^2}} < 1.$ (Eq. S20) is the form of interaction coefficients we

1262 chose in our model.

1263 A family of vectors u_i verifying (Eq. S19a,b) always exists as long as the dimension of the 1264 resource space verifies $m \ge n$. In words, there must be a number of resource types at equal or 1265 superior to the number of competing species.

Biologically speaking, (Eq. S18) and (Eq. S19a,b) makes competition among species happen as follows: all the species share the same basic needs captured by c. In addition to these basic needs, each species i has some specific additional needs captured by u_i , which differentiate its ecological behavior (and its niche) from the others'.

1270 What makes our model not absolutely general is imposing (Eq. S19b), which states that 1271 differences among species in their resource consumption must be orthogonal according to *M*. 1272 We believe that this particular case is a fruitful and simple starting point for the study 1273 multispecies competition models.

1274 **References**

1275 Chesson, P. (1990). MacArthur's consumer-resource model. *Theor. Popul. Biol.* 37, 26-38.

1276 Chesson, P. (1994). Multispecies competition in variable environments. *Theor. Pop. Biol.*, 45,
1277 227-276.

1278 1279	Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. Annu. Rev. Ecol. Evol. Syst., 31, 343–358.
1280 1281	MacArthur, R. (1970). Species packing and competitive equilibrium for many species. <i>Theor. Pop. Biol.</i> , 1, 1-11.
1282	
1283	
1284	
1285	
1286	

1287 Appendix S3 Supplementary results

1288

1289 Additional scenarios considering different dispersal strategies

1290 First, we included a colonization-competition trade-off, where species chance to disperse was 1291 inversely proportional to their ks. So, species that are strong competitors are poor dispersers (as already shown by empirical studies, as Cadotte 2007). Second, we simulated a 1292 restricted/versatile scenario, where species chance to disperse is proportional to their thetas. 1293 1294 In this case, species with higher dependence to common resources (generalists with high thetas) would come first and late colonizers would be those with specialized resource 1295 1296 requirements (Bonte et al. 2003). This simulates the case where the resources for generalist 1297 species are available more quickly (as would be expected if a similar species already occurs in that community). As high theta means that a species competes for the common resource, it 1298 1299 makes sense that this species would reach a patch more quickly, because its resources would always be available (Reinhardt et al. 2005). So, in this case, marginal and specialized species 1300 1301 would come late in the colonization sequence.



Figure S1. Results of richness, Jaccard dissimilarity and species dispersion metrics when we varied the number of sequential colonization events during community assembly in the colonization-competition trade-off scenario. Community assembly was performed using a species pool with medium niche differences and fitness values at the species pool scale. We first applied indices SES-MNTD and SES-MPD separately to niche distances and fitness distances between species and then to the overall functional distances which combines niche and fitness as defined in the main text.



Figure S2. Results of richness, Jaccard dissimilarity and species dispersion metrics when we varied the number of sequential colonization events during community assembly in the restricted/versatile scenario. Community assembly was performed using a species pool with medium niche differences and fitness values at the species pool scale. We first applied indices SES-MNTD and SES-MPD separately to niche distances and fitness distances between species and then to the overall functional distances which combines niche and fitness as defined in the main text.

1327 Additional results using different functional diversity metrics

1334

We calculated the Functional Dispersion (distance to centroid). We did that calculating FDisp (Laliberté and Legendre 2010) and then using a randomization approach (Independent swap by Gotelli and Entsminger 2003) in the distance matrix to provide a null model comparison. The values in the figure below represent the number of times the real result was larger than the null values, so values close to one means strong overdispersion (the real value was larger than most of randomization). The results were similar to those of SES.MNTD and SES.MPD.



1335 Figure S3. Results for SES.MNTD, SES.MPD and SES.FDisp. The first box shows the results of SES.MNTD, the second of SES.MPD and the third of the new SES.FDisp. The 1336 1337 horizontal line represents the null expectation. Values higher than the null expectation represent more differences than expected by random and lower values the opposite. The 1338 1339 general pattern found in our study and used to support most of our discussion holds. Sampling niche traits will always lead to trait oversdispersion, fitness traits will be prone to 1340 1341 show clustering and random pattern and overall species distance, calculated using both niche 1342 related and fitness related traits will tend strongly to overdispersion. 1343 1344 1345 1346 1347 References 1348



- dispersal in specialist spiders from fragmented landscapes. Proceedings of the Royal
- 1351 Society of London B: Biological Sciences 270: 1601-1607.
- 1352 Cadotte, M. W. 2007. Concurrent niche and neutral processes in the competition-
- 1353 colonization model of species coexistence. Proceedings of the Royal Society of
- London B: Biological Sciences 274: 2739-2744.
- 1355 Reinhardt, K., Köhler, G., Maas, S., and P. Detzel. 2005. Low dispersal ability and habitat
- specificity promote extinctions in rare but not in widespread species: the Orthopteraof Germany. Ecography 28: 593-602.
- Laliberté, E., and P. Legendre. 2010. A distance based framework for measuring functional
 diversity from multiple traits. Ecology 91: 299-305.
- 1360 Gotelli, N. J., and G. L. Entsminger. 2003. Swap algorithms in null model
- 1361 analysis. Ecology 84: 532-535.
- 1362
- 1363