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► To cite this version:

Fabien Laroche, Philippe Jarne, Thomas Perrot, Francois Massol. The evolution of the competition– dispersal trade-off affects alpha-and beta-diversity in a heterogeneous metacommunity. Proceedings of the Royal Society B: Biological Sciences, 2016, 283 (1829), pp.20160548. 10.1098/rspb.2016.0548 . hal-01344735

HAL Id: hal-01344735

<https://hal.science/hal-01344735>

Submitted on 16 May 2020

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PROCEEDINGS B

The evolution of the competition-dispersal trade-off affects α and β -diversity in a heterogeneous metacommunity

Journal:	<i>Proceedings B</i>
Manuscript ID	RSPB-2016-0548.R1
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Laroche, Fabien; CEFE; AgroParisTech-ENGREF; Irstea Centre de Nogent-sur-Vernisson; Sveriges lantbruksuniversitet Jarne, Phillippe; CEFE Perrot, Thomas; CEFE; INRA; CNRS Massol, Francois; Laboratoire GEPV, CNRS UMR 8198; CEFE
Subject:	Ecology < BIOLOGY, Evolution < BIOLOGY, Theoretical biology < BIOLOGY
Keywords:	neutral theory, trade-off, metacommunity, species diversity, evolutionary branching, T-statistics
Proceedings B category:	Population and community Ecology

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Manuscripts

1 **Title:**

2 **The evolution of the competition-dispersal trade-off affects α and β -diversity in a**
3 **heterogeneous metacommunity**

4

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21 **ABSTRACT**

22 Difference in dispersal ability is a key driver of species coexistence in metacommunities.
23 However, the available frameworks for interpreting species diversity patterns *in natura* often
24 overlook trade-offs and evolutionary constraints associated with dispersal. Here we build a
25 metacommunity model accounting for dispersal evolution and a competition-dispersal trade-
26 off. Depending on the distribution of carrying capacities among communities, species
27 dispersal values are distributed either around a single strategy (ESS; evolutionarily stable
28 strategy), or around distinct strategies (EB; evolutionary branching). We show that limited
29 dispersal generates spatial aggregation of dispersal traits in ESS and EB scenarios, and that
30 the competition-dispersal trade-off strengthens the pattern in EB scenario. Importantly,
31 individuals in larger (resp. smaller) communities tend to harbour lower (resp. higher)
32 dispersal, especially under the EB scenario. We explore how dispersal evolution affects
33 species diversity patterns by comparing those from our model to the predictions of a neutral
34 metacommunity model. The most marked difference is detected under EB, with distinctive
35 values of both alpha- and beta-diversity (e.g., the dissimilarity in species composition between
36 small and large communities was significantly larger than neutral predictions). We conclude
37 that, from an empirical perspective, jointly assessing community carrying capacity with
38 species dispersal strategies should improve our understanding of diversity patterns in
39 metacommunities.

40

41 **KEY-WORDS**

42 Neutral theory; trade-off; metacommunity; species diversity; evolutionary branching; null
43 models; coalescence; T-statistics.

44

45 **MAIN TEXT**46 **INTRODUCTION**

47 Ecological differentiation is considered as a driver of stable coexistence among
48 competing species since the origin of community ecology [1–3]. In this context, resource
49 partitioning plays an important role, but numerous theoretical [4–6] and experimental [7,8]
50 studies emphasized that trade-offs between local competitive ability and dispersal of species
51 in patchy environments (so-called “competition-colonization” or “competition-dispersal”
52 trade-offs) also favour coexistence. Both empirical studies and field surveys suggest that these
53 trade-offs are a distinctive characteristic of communities from many natural systems [9,10],
54 and are sometimes associated with wide variation in dispersal among species belonging to the
55 same community (e.g., [11] for the tree community of Barro Colorado Island). However,
56 whether (and how) they affect patterns of species diversity in natural communities remains
57 debated [12,13]. One reason is that studies trying to explain such patterns using empirical data
58 on dispersal variation and potential trade-offs with competitiveness remain scarce and focused
59 on simple communities including a few species at best [12,13]. Gathering such data is indeed
60 a highly demanding endeavour in complex natural communities.

61 A less demanding, though more indirect, approach to the role of trade-offs on species
62 diversity patterns is the “pattern-to-process” approach in which these patterns are used to infer
63 the underlying processes, and therefore to distinguish among coexistence theories. However,
64 the theory of species coexistence based on the competition-dispersal trade-off has mostly been
65 developed in terms of “patch dynamics” [5,14,15], considering monospecific communities
66 and focusing on species diversity at the “metacommunity” scale only. Such assumptions are
67 far from realistic for most natural systems and prevent studying diversity patterns within sites.
68 The metacommunity framework provides more general models, giving more or less weight to
69 basic processes such as dispersal, demographic stochasticity, or competition (see [15] for a

70 review). In particular, neutral models [16–18] constitute an interesting entry into
71 metacommunity dynamics: they assume ecological equivalence of species [6] and attribute a
72 major role to the balance between demographic stochasticity and dispersal. Importantly, these
73 models yield accurate quantitative descriptions of community structure [19]. An outstanding
74 example is the fit of a neutral model to the rank-abundance diagram of tropical trees in Barro
75 Colorado Island [20]. We suggest here that neutral models could be used for building
76 predictions about the effects of interspecific competition-dispersal trade-offs on diversity
77 patterns, providing a more sophisticated basis than patch-dynamics models for pattern-to-
78 process approaches.

79 We only know of two studies that assessed the impact of interspecific heterogeneity of
80 dispersal on species diversity patterns by comparing these patterns to neutral predictions. Liu
81 et al. [21] introduced several dispersal levels in an otherwise neutral model. They showed that
82 the rank-abundance diagram of a community could not be used to detect heterogeneous
83 dispersal because this pattern is already very well predicted by a purely neutral model. Janzen
84 et al. [22] showed that using seed-dispersal traits when analysing rank-abundance patterns of
85 tree species in Barro Colorado Island could lead to reject a purely neutral model in favour of
86 an alternative hypothesis involving interspecific dispersal. Both [21] and [22] considered the
87 effect of interspecific heterogeneity of dispersal on community structure through variation in
88 propagule pressure: species with higher dispersal exert a stronger propagule pressure and are
89 therefore better represented locally. However, in such models, dispersal does not trade off
90 with local competitive ability (assumed to be identical among species): species with higher
91 dispersal always thrive in all communities. The conditions for regional coexistence are
92 unfortunately not considered in these studies which focus on species diversity within
93 communities. Introducing a metacommunity structure in which species can coexist within
94 local communities and a competition-dispersal trade-off in models such as those of [21,22]

95 should allow to study conditions for the regional coexistence of dispersal strategies as a result
96 of a trade-off with local competition. This is what is done in our study.

97 Dispersal has a genetic basis in many species [23–25] and can evolve quickly under
98 selection [26,27], suggesting that interspecific variation along a competition-dispersal trade-
99 off should not only be ecologically stable, but also evolutionarily stable, at the
100 metacommunity scale. The evolution of dispersal has been considered in several theoretical
101 studies [28,29], though mostly in single-species metapopulations, especially to explore
102 whether dispersal is stabilised by selection around an evolutionarily stable strategy (ESS), or
103 whether it can diversify toward several strategies (evolutionary branching; EB). We are
104 particularly interested in the latter scenario in which the coexistence among strategies verifies
105 both ecological and evolutionary stability. Several processes can generate EB on dispersal
106 (*e.g.* spatial and temporal fluctuations of environmental conditions [30–32]). In particular,
107 Massol et al. [33] showed that variation in the strength of kin selection due to variation in
108 carrying capacity among populations is sufficient to generate disruptive selection on dispersal
109 and EB, without calling for fluctuations. Their model includes both an explicit
110 metapopulation structure and a competition-dispersal trade-off. We upscaled it to
111 metacommunity level which allowed us to explore whether dispersal polymorphism has an
112 effect on diversity within communities and dissimilarity among communities compared to a
113 neutral model without dispersal polymorphism. This extends the current framework for
114 interpreting species distribution to the competition-dispersal coexistence theory.

115

116 **METHODS**

117 **Model with dispersal evolution (model M_1)**

118 Model M_1 simultaneously describes the evolutionary dynamics of dispersal and the
119 temporal change in species diversity in a metacommunity. Individuals share several attributes:

120 a species label, a dispersal parameter d , the cost of dispersal c , the probability (μ) and
121 magnitude (σ) of mutations on dispersal, and the speciation probability ν . These attributes are
122 real numbers between 0 and 1, except σ which lies between 0 and 0.1. Individuals belong to
123 communities which are described by their carrying capacity K (*i.e.* the number of individuals
124 they can harbour). The metacommunity is made of N communities which can have different
125 carrying capacities.

126 Mortality occurs continuously, and dead individuals are immediately replaced through
127 a lottery process. Each death-replacement cycle starts with a “death” event: a randomly
128 chosen individual is removed from the metacommunity. Each individual constantly produces
129 a very large number of propagules normalised to 1 for the lottery. A fraction $1 - d$ of
130 propagules remains in the community and a proportion d is dispersed in the metacommunity,
131 which induces a trade-off between local competition and dispersal. A proportion c of
132 dispersed propagules are lost (dispersal cost). Dispersed propagules have equal chance of
133 reaching all communities, meaning that an individual exports $d(1 - c)/N$ propagules to each
134 community. The model is therefore spatially implicit. A dead individual is replaced by either
135 a local or an imported propagule in proportion to their occurrence (lottery). The new
136 individual has the same dispersal probability as its parent (d) with probability $1 - \mu$. When
137 mutation occurs (probability μ), the dispersal probability differs from that of the parent by
138 $\pm\sigma \min(10d, 10(1 - d), 1)$, σ being the maximum amplitude of a mutation. This function
139 was chosen to ensure both (i) a non-biased change in dispersal whatever the value of d and
140 (ii) a mutant dispersal probability within the (0,1) interval ($\sigma = 0.01$ in our simulations). In
141 addition, with probability ν , the new individual belongs to a new species that never occurred
142 before in the metacommunity (*i.e.* point speciation; see [18]). Speciation has no effect on
143 dispersal and does not interact with the mutation dynamics. A new cycle then starts. Calling

144 $J = N\bar{K}$ the total number of individuals in the metacommunity, the expected life-time of an
 145 individual is J cycles, such that a “generation” can be defined as J cycles.

146 Following [33, equations 4 and 5], the mean \bar{K} , squared coefficient of variation
 147 $\gamma_2 = \mathbb{E}[(K - \bar{K})^2]/\bar{K}^2$ and standardized skewness $\gamma_3 = \mathbb{E}[(K - \bar{K})^3]/(\gamma_2^{3/2}\bar{K}^3)$ of carrying
 148 capacity distribution among communities determine whether EB or ESS of dispersal should
 149 occur. Here we studied metacommunities in which communities can harbour only two
 150 carrying capacities K_1 and K_2 ($K_1 < K_2$). We note π_1 the proportion of communities with
 151 carrying capacity K_1 . We selected two examples of metacommunities (“symmetric” and
 152 “asymmetric”) corresponding to the ESS and EB scenarios on dispersal (Table 1 and
 153 Appendix 1). The symmetric metacommunity is made of an equal number of small and large
 154 communities ($\pi_1 = 0.5$), while the asymmetric one is essentially made of small communities
 155 ($\pi_1 \approx 0.97$). These metacommunities display the same \bar{K} and γ_2 values, as well as the same
 156 number of communities (N). Keeping \bar{K} and N constant yields the same overall number of
 157 individuals in the metacommunity, which implies the same rate of occurrence of new species
 158 and the same singular value of dispersal $d^* = \min(1/(\bar{K}(c + \gamma_2)), 1)$ in the two
 159 metacommunities (i.e. the value at which branching or evolutionary stability may occur, see
 160 [33]). We set the mean carrying capacity of communities to $\bar{K} = 8$ and the number of
 161 communities in the metacommunity to $N = 1110$ (see Appendix 1), so that both
 162 metacommunities contained $J = 8880$ individuals.

163 At the beginning of the first cycle, all individuals harboured the same dispersal value
 164 set to the singular value d^* . Species identities were attributed using the urn sampling scheme
 165 developed for the neutral model of species diversity with multiple communities [34]. In both
 166 cases, mutation and speciation parameters were set to: $\mu = 0.01, \sigma = 0.01, \nu = 10^{-4}$. These
 167 parameters were chosen so as to (i) remain close to the assumption of adaptive dynamics
 168 (limiting the rate and size of mutations of dispersal), (ii) ensure evolutionary dynamics that

169 are fast enough to exhibit the outcomes of interest with simulations of tractable length and
170 size, and (iii) keep a separation of timescales between speciation and mutation processes. We
171 explored three values of dispersal cost ($c = 0, 0.1$ and 0.5). As the results were qualitatively
172 similar, we only reported results for $c = 0.1$ in the main text (full results in Appendix).

173 For both symmetric and asymmetric metacommunities, 100 independent simulations
174 were run over 20000 generations (*ca.* 1.77×10^8 death-replacement cycles), a value large
175 enough to reach a stationary dispersal distribution. Simulations were run using the Java
176 programming language (source code DOI: 10.6084/m9.figshare.3145831).

177

178 **Neutral model (model M_0)**

179 Model M_0 is a particular case of model M_1 in which all individuals from the
180 metacommunity display the same dispersal value and dispersal does not evolve (*i.e.* $\mu = 0$). M_0
181 is thus a neutral model in which individual dispersal is explicitly described. Expected patterns
182 of species diversity can be derived analytically in this model using a coalescent approach
183 (inspired from [35]; Appendix 4).

184

185 **Trait and species diversity patterns**

186 We explored the spatial structure of dispersal trait in the final state of simulations
187 produced by model M_1 using T -statistics ([36]), a tool to decompose the metacommunity-
188 wide variance of dispersal into the relative contributions of several levels of organization:
189 individual (I), community (C) and metacommunity (R, for regional). We focused on $T_{IC/IR}$,
190 the proportion of dispersal variance at metacommunity level explained by variation of
191 individual dispersal within communities. Low $T_{IC/IR}$ means that individuals from a
192 community tend to be similar, which we call “dispersal clumpiness”. We tested whether
193 $T_{IC/IR}$ is lower than expected under two null models using a randomization procedure. First,

194 we preserved the species label and dispersal value of individuals, but permuted their
195 community identity among communities (keeping community size constant). Under the
196 second model, we permuted dispersal values among species but preserved the occurrence and
197 relative abundances of species in communities. In this second test, we overlooked
198 intraspecific variation by first attributing to individuals the average metacommunity trait
199 value of their species. Randomization proceeded such that individuals from species A were
200 attributed the trait from species B, etc. The mean observed $T_{IC/IR}$ values in the 100 replicated
201 simulations was compared to the mean of the null distribution, obtained by applying the
202 randomization procedure to each simulation output and re-computing $T_{IC/IR}$.

203 When comparing predictions from models M_0 and M_1 in terms of species diversity
204 patterns, we focused on measures of (i) diversity within communities (α -diversity), (ii)
205 differentiation among communities (β -diversity) and (iii) diversity at metacommunity scale
206 (γ -diversity). We defined $D_\alpha(K_i)$ as the probability that two individuals sampled in the same
207 community with carrying capacity K_i belong to different species. $D_\alpha(K_i)$ is a standard index
208 of diversity usually called the Simpson index [37]. To evaluate the differentiation between
209 community pairs, we used $D_\beta(K_i, K_j)$ defined as the probability that two individuals drawn
210 from distinct communities with carrying capacities K_i and K_j belong to different species. D_γ ,
211 defined as the probability that two individuals randomly sampled in the metacommunity
212 belong to different species, was used at the metacommunity scale.

213

214 **RESULTS**

215 When allowing dispersal to evolve (model M_1), our simulations corroborated the
216 theoretical predictions of adaptive dynamics (Figure 1). In the symmetric metacommunity
217 (metacommunity 1), variation in dispersal remained concentrated around d^* , in agreement
218 with the ESS prediction. In the asymmetric metacommunity (metacommunity 2), two distinct

219 values emerged due to the evolutionary dynamics, in agreement with the EB prediction. The
220 difference between these dispersal values decreased with the dispersal cost c (Appendix 2,
221 Figure A2.1) and increased with the square coefficient of the variation in carrying capacity
222 (γ_2 ; Appendix 2, Figure A2.2). Following species composition of the asymmetric
223 metacommunity in time during and after dispersal branching (Figure 2) further showed that (i)
224 species that appeared before branching could persist in both branches long after branching,
225 but ultimately went extinct because of speciation and demographic stochasticity; (ii) species
226 that appeared after branching stayed in their original branch. No species was present in both
227 evolutionary branches at the end of 95 of our 100 replicates; it is therefore possible to
228 characterize “dweller” and “drifter” species, harbouring low and high dispersal values
229 respectively. The situation is very different under the ESS scenario in which, by definition, all
230 species had similar dispersal values at all time.

231 The proportion of variance of dispersal among individuals within communities was
232 significantly lower than expected under a random permutation of individual position (*i.e.*
233 $T_{IC/IR}$ was significantly lower than random expectation using the first randomization
234 procedure; Figure 3A), especially in the asymmetric metacommunity. When permuting
235 species traits while preserving their abundance in each community (Figure 3B), $T_{IC/IR}$ under
236 the ESS scenario was not significantly different from the randomized value while a
237 significantly lower value was observed under the EB scenario. We further observed that the
238 average dispersal was significantly larger in communities with small carrying capacity than in
239 those with large carrying capacity in the two metacommunities (Figure 3C), a pattern that we
240 call the “carrying capacity - dispersal relationship” below. Appendix 3 provides an analytical
241 argument to explain the emergence of this pattern. The carrying capacity – dispersal
242 relationship was much less pronounced in the symmetric metacommunity (ESS) than in the

243 asymmetric one (EB). All these results are robust to variation in the dispersal cost (Appendix
244 3, Figures A3.1 and A3.2).

245 Under the ESS scenario, all species harboured similar dispersal strategies, and the
246 carrying capacity-dispersal relationship was weak (but still significant). We therefore
247 expected species diversity patterns (D_α , D_β and D_γ) to closely match the predictions of our
248 neutral model M_0 . Under the EB scenario, dweller and drifter species emerged, as well as a
249 strong carrying capacity-dispersal relationship. We therefore expected species diversity
250 patterns to strongly deviate from model M_0 predictions. In particular, we expected a higher
251 $D_\beta(K_1, K_2)$ than under model M_0 because small communities are occupied by drifter species
252 while large communities are occupied by dweller species. We derived analytical expressions
253 of $D_\alpha(K_i)$, $D_\beta(K_i, K_j)$ and D_γ in model M_0 (Appendix 4) which were validated using
254 simulations (Figure A4.2). $D_\alpha(K_i)$ and $D_\beta(K_i, K_j)$ depend on the dispersal rate (d^*), the
255 dispersal cost (c), the speciation rate (ν) and the mean, variance and asymmetry of the
256 distribution of the carrying capacities across the metacommunity, but not on the carrying
257 capacities K_i and K_j . Higher asymmetry of the distribution always had a negative impact on
258 D_α , D_β and D_γ (Figure A4.3). In the examples considered here, in which the coefficient of
259 variation was kept constant but asymmetry varied, the neutral diversity at community (D_α)
260 and metacommunity levels (D_γ) as well as the dissimilarity among communities (D_β) in the
261 symmetric metacommunity were thus predicted to be higher than in the asymmetric
262 metacommunity (Figure 4).

263 We computed the unbiased \hat{D} estimates (defined in Appendix 5) of $D_\alpha(K_1)$,
264 $D_\alpha(K_2)$, $D_\beta(K_1, K_1)$, $D_\beta(K_1, K_2)$, $D_\beta(K_2, K_2)$ and D_γ from our simulations of model M_1 and
265 compared them to the analytical predictions of M_0 (Figure 4). In the symmetric
266 metacommunity (dispersal ESS), $\hat{D}_\alpha(K_1) \approx \hat{D}_\alpha(K_2)$, and $\hat{D}_\beta(K_1, K_1) \approx \hat{D}_\beta(K_1, K_2) \approx$

267 $\widehat{D}_\beta(K_2, K_2)$, in line with neutral predictions. However, all \widehat{D} estimates were lower than the
268 neutral predictions. In the asymmetric metacommunity (EB; Figure 4), the \widehat{D}_α s were also
269 similar between small and large communities, in line with the predictions of model M_0 , but
270 this time larger than the neutral expectations. $\widehat{D}_\beta(K_1, K_2)$ and $\widehat{D}_\beta(K_2, K_2)$ were, as expected,
271 higher than the neutral expectations. These deviations from the neutral predictions of both \widehat{D}_α
272 and \widehat{D}_β resulted in a larger \widehat{D}_γ than predicted by the neutral model (Figure 4). Note also that
273 $\widehat{D}_\beta(K_1, K_1)$ and $\widehat{D}_\alpha(K_1)$ were very similar in the asymmetric metacommunity (Figure 4),
274 indicating that, when sampling two individuals in small communities, the probability of
275 getting two different species did not depend on whether individuals were drawn from the
276 same or from different communities. These results were robust to changing the dispersal cost
277 (Appendix 5, Figures A5.1 and A5.2).

278

279 **DISCUSSION**

280 **Dispersal in metacommunities**

281 We built a metacommunity model including dispersal evolution which reproduces the
282 central result obtained by [33] at the metapopulation scale: increasing asymmetry in the
283 distribution of carrying capacities generates variance in the strength of kin competition among
284 communities, which triggers evolutionary branching and the emergence of distinct dispersal
285 strategies in the metacommunity. We could therefore compare an ESS scenario in which
286 individual dispersal shows little variation around a single value (symmetric metacommunity)
287 and an EB scenario in which dispersal is distributed around two distinct levels (asymmetric
288 metacommunity).

289 Our analysis of dispersal distribution within and among communities showed that
290 under both scenarios, a negative carrying capacity - dispersal relationship emerges. This
291 pattern stems from the three following effects. First, all communities have similar immigrant

292 pool compositions because dispersal is not limited by distance in our model. Second, in small
293 communities, the temporal dynamics of average species abundances in these small
294 communities are mostly driven by immigration, and are similar to those of the immigrant
295 pool. Third, the deterministic local competition effect dominates in large communities, which
296 induces a shift of relative abundances toward the dominance of low dispersers and the
297 extinction of high dispersers (*i.e.* competitive exclusion).

298 The carrying capacity-dispersal relationship echoes several observations on within-
299 species dispersal polymorphism in natural metapopulations. For example, a majority of
300 migrants originates from small ephemeral patches, rather than from large patches, in a rock
301 pool metapopulation of the cladoceran *Daphnia magna* [38]. However, a competition-
302 dispersal trade-off may not be the only driver of such patterns in natural metapopulations as
303 variation in both age (when extinctions occur) and connectivity of populations play an
304 important role in the distribution of dispersal phenotypes among populations [39]. Whether
305 the carrying capacity - dispersal relationship occurs at the interspecific level in natural
306 metacommunities is less documented to date. Our work predicts that species occurring
307 preferentially in communities with large (resp. small) carrying capacities should be dwellers
308 (resp. drifters). A comparison of traits assumed to be good proxies of dispersal, such as
309 dispersal attributes of seeds in plant communities (see [40] for an example in grassland
310 communities) might be a first approach to test this prediction. More refined statistical
311 approaches based on dispersal kernel estimation [11,41] is a further possibility. A
312 combination of genetic and demographic data collected in several species might also return
313 relevant information on dispersal, as already done in metapopulations of single species (*e.g.*,
314 [42])

315 A strong carrying capacity-dispersal relationship (like in EB scenario) has potential to
316 generate dispersal clumpiness, as small (resp. large) communities tend to harbour more

317 drifters (resp. dwellers) than expected under random permutation of individual in space.
318 However, dispersal clumpiness can emerge even in the absence of strong carrying capacity-
319 dispersal relationship as exemplified in the ESS scenario. This stems from the fact that when
320 dispersal is limited, individuals which are in the same community tend to be more closely
321 related than individuals randomly sampled at the metacommunity scale. This generates
322 clumpiness of both species [43] and values of heritable traits, which in turn yields a lower
323 $T_{IC/IR}$ than expected when permuting individuals across the metacommunity. Interestingly,
324 this should caution against interpreting all significantly low $T_{IC/IR}$ as signals of some kind of
325 “environmental filtering” associated to the considered trait (as suggested by [36]) when using
326 a null model randomizing individual position in space. By contrast, our second randomizing
327 procedure (permuting average species trait only) exhibits two properties addressing the above-
328 described limits: it preserves the variation of species abundances among communities and it
329 removes the effects of increased relatedness within populations by considering average
330 species traits. Under the ESS scenario, the variance within communities was not significantly
331 lower than the one expected under the null model, which corroborates the idea that the
332 significantly low $T_{IC/IR}$ observed when randomizing individual positions is mostly due to the
333 effect of limited dispersal and not to dispersal polymorphism (which is limited in this case).
334 Under the EB scenario, the dispersal strategies were still significantly more similar within
335 communities than predicted by the null model. Permuting average species traits can therefore
336 be used to disentangle the effects of limited dispersal on spatial patterns of dispersal (null
337 model not rejected) from those of dispersal polymorphism (null model rejected), and should
338 be preferred to permuting individual positions whenever limited dispersal is thought to play a
339 role in diversity patterns.

340

341 **Neutral predictions on species diversity patterns**

342 Our neutral model makes two important predictions about species diversity patterns.
343 First, α - and β -diversity should not vary (in expectation) among communities with different
344 carrying capacities. In several neutral metacommunity models, Simpson diversity (used here)
345 can vary among patches [44,45]. However, this variation is mostly explained by differences in
346 connectivity (*i.e.* the number of immigrants per generation) among patches induced by
347 specific network structures. As we were primarily interested in the relationship between the
348 evolutionary dynamics of dispersal and diversity patterns, we focused on a simple spatial
349 structure in which connectivity is similar between all patches irrespective of their carrying
350 capacity, a situation for which we could derive evolutionary predictions. Our model might be
351 extended to more complex community networks in which the neutral expectations have
352 already been derived and that better describe the spatial structure of some real
353 metacommunities, such as dendritic networks for rivers [46,47]. The limiting step here would
354 be to derive eco-evolutionary predictions about dispersal polymorphism in complex networks
355 with variable connectivity among patches, a point that has little been explored up to now [48].

356 Second, our neutral model predicts that species γ -diversity should decrease with the
357 asymmetry of the carrying capacity distribution in the metacommunity. This can be intuitively
358 explained by the fact that, in more asymmetric metacommunities, drift is stronger because
359 more individuals belong to small communities. Here, we focused on the prediction about
360 asymmetry as it is the feature of carrying capacity distribution that discriminates dispersal
361 evolution scenarios [33]. Yet, the analytical results derived from our neutral model may allow
362 a more comprehensive exploration of the effects of carrying capacity distribution on species
363 γ -diversity (Figure A4.3) and thus contribute to current research in conservation biology, in
364 particular with respect to reserve design [49]. However, this is beyond the scope of the present
365 work.

366 In the two examples of metacommunities considered in our study, we derived neutral
367 predictions about diversity patterns when *a priori* knowing the relevant parameters (carrying
368 capacities and dispersal cost). However, it may not be straightforward to obtain these
369 parameters in natural systems. One alternative would be to fit the neutral model to observed
370 diversity patterns in order to estimate their most likely values. The sampling formulas that
371 have been derived for classic neutral models considering spatially implicit metacommunities
372 allow computing maximum likelihood estimates [34,50,51]. Such a formula is not available for
373 our model, but the carrying capacities of communities and the dispersal cost could be
374 estimated by looking for values that yield predictions about expected diversity and
375 dissimilarity that fit the best to the observed diversity and dissimilarity estimates (e.g., using a
376 least-square approach).

377

378 **Effects of dispersal polymorphism on species diversity**

379 Our neutral predictions (model M_0) incorporate the influence of speciation, drift and
380 limited dispersal. Comparing the neutral predictions of species diversity patterns with model
381 M_1 , in which dispersal can evolve, reveals the additional effects (i) of mutational variance
382 around the selective optima in the ESS scenario and (ii) of disruptive selection of dispersal in
383 the EB scenario. To our knowledge, our study is the first to suggest studying the effects of a
384 competition-dispersal trade-off as an evolutionarily driven deviation from the neutral theory
385 of metacommunity assembly.

386 In the ESS scenario (symmetric metacommunity), both the diversity within
387 communities and the dissimilarity among communities do not depend on carrying capacity,
388 which is consistent with the neutral predictions. This was rather expected as species are
389 distributed around the same dispersal value, with some variation due to mutation, leading to
390 metacommunity dynamics close to neutrality. However, lower diversity and lower

391 dissimilarity than expected under a neutral model suggest that the mutational variance of
392 dispersal generates fitness differences among individuals, which scale up to a slight fitness
393 heterogeneity among species. Slightly maladapted species are more quickly eliminated than
394 expected under the neutral model which yields a lower diversity at the metacommunity scale
395 and consequently decreases both the diversity within communities and the dissimilarity
396 among communities. More generally, our results suggest that when there is a unique selective
397 optimum on a given trait (*i.e.* stabilizing selection), neutral models which overlook intra- and
398 inter-specific variance in this trait may overestimate species diversity.

399 Under EB, the following general picture of the metacommunity emerged: (i) each
400 large community harbours a mostly endemic community of species that are good local
401 competitors but nearly never disperse (dwellers); (ii) drifter species freely disperse across the
402 metacommunity, dominating small communities and maintaining themselves at low frequency
403 through mass effect in large communities although they are locally outcompeted by dwellers.
404 From point (i) derives the higher dissimilarity among large communities than expected under
405 the neutral model. Point (ii) explains why the diversity of small communities equals the
406 dissimilarity among small communities. The mass effect of drifters in large communities
407 explains why diversity/dissimilarity in small communities ($D_\alpha(K_1)$) matches the diversity
408 observed in a single large community ($D_\alpha(K_2)$) although the former includes many more
409 individuals. We also emphasize that, when EB occurs, both α - and β -diversities are higher
410 than predicted by the neutral model. Dispersal polymorphism increases the species
411 coexistence potential at metacommunity scale.

412 Our work suggests that the study of diversity patterns in metacommunities would
413 greatly benefit from documenting dispersal traits of species, so as to identify dwellers and
414 drifters. This point was previously made by Janzen et al. [22] in their study of the Barro
415 Colorado tropical tree community: they concluded from combining local abundances of

416 species with seed dispersal traits that immigration was stronger for biotically dispersed tree
417 species (which would therefore be drifters) than for abiotically dispersed ones (which would
418 therefore be dwellers). Importantly enough, biotically dispersed species are dominant in Barro
419 Colorado island. This point cannot be discussed in Janzen et al. framework, as dispersal does
420 not trade-off with any other features (it is a structural property of their model that drifters
421 dominate in any community). By contrast, our model suggests a biological interpretation of
422 drifters' dominance: the carrying capacity of Barro Colorado island may be too small to let
423 dwellers reach large enough population sizes to durably settle and counterbalance the
424 immigration of drifters.

425 Beyond analyzing a single community, testing whether small communities (i) have
426 more similar species composition than they have with large communities and (ii) harbour
427 species with higher dispersal abilities than large communities may reveal that a competition-
428 dispersal trade-off affects species coexistence at the metacommunity scale. In addition, the
429 EB scenario of our model illustrates how considering dispersal may contribute to avoid
430 misinterpreting species diversity patterns. First, dwellers species are abundant in one or a few
431 large communities and absent elsewhere, but this is not due to local environmental filtering or
432 adaptation. Dwellers should here show the same fitness in all communities, irrespectively of
433 size. Second, large communities simultaneously harbour dwellers and drifters the relative
434 abundances of which fluctuate around stable values in time (results not shown), and this is not
435 due to some local coexistence mechanisms but rather to mass effect from the metacommunity.

436

437 **Conclusion**

438 To our knowledge, our study proposes the first theoretical model integrating dispersal
439 evolution in a multi-species context and deriving predictions about species diversity patterns.
440 Interestingly it includes three of the four paradigms of metacommunity assembly identified by

441 Leibold et al. [15]: it simultaneously borrows from (i) the “patch-dynamics” view by
442 considering a competition-dispersal trade-off as a coexistence mechanism, (ii) the “mass-
443 effect” view as drifter species can persist in patches due to immigration, although they are less
444 fit locally, and (iii) the neutral view as species diversity in the metacommunity ultimately
445 stems from an equilibrium between speciation and stochastic extinction. Our approach should
446 now be extended to other traits contributing to the local adaptation of species in patches with
447 heterogeneous environmental conditions (see [52]) but keeping the focus on the evolutionary
448 and ecological significance of the considered polymorphisms, as we did here with dispersal.
449 This would integrate the fourth metacommunity paradigm, species sorting [15], and might
450 pave the way to an unified framework for pattern-based approaches of metacommunity
451 assembly processes.

452

453 **COMPETING INTEREST STATEMENT**

454 The authors declare no competing interest.

455 **AUTHORS' CONTRIBUTION**

456 FL, PJ & FM built the project. FM did the analysis of dispersal evolution. TP ran the
457 simulations. FL derived the neutral predictions and analysed the simulations. FL, PJ and FM
458 wrote the paper.

459 **ACKNOWLEDGEMENTS**

460 Many thanks are due to P. David, N. Loeuille, S. Maurice, F. Munoz, and R. Vitalis for
461 discussions and to F. Altermatt, E. Klein, S. Pavoine, O. Ronce and C. Vacher for their useful
462 comments on the manuscript. We also thank associate editor O. Gaggiotti and two anonymous
463 referees for significant improvements during the revision process. We thank the CEFE
464 (Center for Evolutionary and Functional Ecology) and particularly M.-C. Quidoz (SIE
465 platform) for access to computational resources.

466 **FUNDING**

467 FL was supported by fellowships from AgroParistech, the Agropolis foundation and the
468 Swedish University of Agricultural Science, and by money from IRSTEA. TP was supported
469 by a fellowship from the Université de Montpellier. This work was supported by money from
470 CNRS to PJ and FM, and from the French ANR (AFFAIRS project in the BIOADAPT
471 program – P.I.: Dr. P. David – grant n° 12-ADAP-005; ARSENIC project – P.I.: Dr. F.
472 Massol – grant n° 14-CE02-0012).

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587

588 **FIGURE AND TABLE CAPTIONS**

589

590 **Table 1:** Parameters of symmetric and asymmetric metacommunities, corresponding to the
591 evolutionary predictions and summary statistics of simulations. The two metacommunities
592 verifies: $\bar{K} = 8$ and $\gamma_2 = 9/16 \approx 0.56$, $N = 1110$ patches. π_1 represents the proportion of
593 patches with carrying capacity K_1 . In both cases, other parameters are set to: $\mu = 0.01$, $\sigma =$
594 0.01 , $\nu = 10^{-4}$, $c = 0.1$. ESS: evolutionary stable strategy; EB: evolutionary branching.

595

596 **Figure 1:** Examples of dispersal distributions through time in model M_1 for symmetric (panel
597 A) and asymmetric metacommunity (panel B) respectively (see Table 1 for metacommunity
598 features). One simulation run is represented in each panel. The grey shades refer to
599 individuals' density when all species are pooled together (null in the white areas). Time is
600 given in generation numbers. Parameters describing dispersal evolution are $\mu = 0.01$ and
601 $\sigma = 0.01$, and the cost of dispersal is $c = 0.1$.

602

603 **Figure 2:** Monitoring of dispersal in three species from the asymmetric metacommunity
604 during the simulation presented in Figure 1B (out of 506 species observed over the whole
605 simulation). Each species is represented by a shade of grey. A grey dot is drawn at (d, t) if an
606 individual of the considered species with trait d occurs in the community at generation t . The
607 species in light grey is initially present before branching and persists after branching, but goes
608 extinct in the lower branch. The other two species appear after branching through speciation,
609 in a single branch.

610

611 **Figure 3:** Analysis of dispersal pattern in symmetric (1) and asymmetric (2)
612 metacommunities. Panel A: Testing $T_{IC/IR}$ using full permutation of individual positions. Bars

613 represent observed (plain bars) and randomized values (striped bars) of $T_{IC/IR}$ at generation
614 20000 averaged over 100 independent simulations. Results for both metacommunity 1 (dark
615 grey bar) and 2 (light grey bar) are shown. For each bar, a 95% confidence interval based on
616 central limit theorem is provided. Panel B: Similar to panel A but overlooking intraspecific
617 variability and permuting only species dispersal values. Panel C: Average dispersal value in
618 small (bars labelled “ K_1 ”) and large (bars labelled “ K_2 ”) communities for metacommunity 1
619 (dark grey) and 2 (light grey). 95% confidence interval of these average value based on
620 central limit theorem approximation are reported for each bar. Testing whether mean dispersal
621 was higher in small communities yielded that the observed difference is statistically
622 significant in both metacommunities (test based on the central-limit theorem Normal
623 approximation; $p=0.0001$ in metacommunity 1, $p < 10^{-12}$ in metacommunity 2).

624

625 **Figure 4:** Estimates and 95% confidence intervals of D_α (panel A), D_β (B) and D_γ (C) in the
626 symmetric and asymmetric metacommunities obtained from model M_I simulations compared
627 to neutral predictions. Grey bars provide the analytical predictions of the neutral model M_0
628 with $d = d^*$ (computed from the left column of table A4.3) for symmetric (dark grey) and
629 asymmetric (light grey) metacommunities. Simulation parameters are given in Table 1. A
630 point is associated to each grey bar, which represents the average estimate value obtained
631 from 100 independent simulations of model M_I . A 95% confidence interval of the expected
632 diversity/dissimilarity value under model M_I is reported around each point.

633

634 **Table 1**

Metacommunity		symmetric	asymmetric
Distribution of carrying capacities	K_1	2	7
	K_2	14	44
	π_1	0.5	36/37
Prediction on dispersal evolution		ESS	EB

635







