



HAL
open science

Dispersal syndromes can link intraspecific trait variability and meta-ecosystem functioning

Allan Raffard, Elvire Bestion, Julien Cote, Bart Haegeman, Nicolas Schtickzelle, Staffan Jacob

► **To cite this version:**

Allan Raffard, Elvire Bestion, Julien Cote, Bart Haegeman, Nicolas Schtickzelle, et al.. Dispersal syndromes can link intraspecific trait variability and meta-ecosystem functioning. *Trends in Ecology & Evolution*, In press, 37 (4), pp.322-331. 10.1016/j.tree.2021.12.001 . hal-03603063

HAL Id: hal-03603063

<https://hal.science/hal-03603063>

Submitted on 9 Mar 2022

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 Dispersal syndromes can link intraspecific trait variability and meta-ecosystem functioning

2

3 Allan Raffard^{1*}, Elvire Bestion², Julien Cote³, Bart Haegeman², Nicolas Schtickzelle¹ &

4 Staffan Jacob²

5

6 ¹ *Université catholique de Louvain, Earth and Life Institute, Biodiversity Research Centre, Louvain-*
7 *la-Neuve, Belgium*

8 ² *Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, Moulis, France.*

9 ³ *CNRS, UPS, IRD, Laboratoire Évolution et Diversité Biologique, UAR 5174, 31062, Cedex 9*
10 *Toulouse, France*

11

12 *allan.raffard@uclouvain.be

13 Trends in Ecology and Evolution, 2022, Vol. 37, No. 4, pages 322-331, DOI:

14 <https://doi.org/10.1016/j.tree.2021.12.001>

15 This manuscript version is made available under the CC-BY-NC-ND 4.0 license

16 <https://creativecommons.org/licenses/by-nc-nd/4.0/>

17

18 **Highlights**

19 Dispersal is a key process for the dynamics and functioning of meta-communities and meta-
20 ecosystems. Meta-ecosystem theory however does not fully integrate the possible effects of
21 dispersal, largely assuming random diffusion of organisms and nutrients, contrasting with
22 rising empirical evidence for intraspecific variability in dispersal strategies.

23 Dispersal is often associated with a suite of phenotypic traits, forming dispersal syndromes.
24 Since phenotypic variability is now acknowledged as a key factor mediating ecosystem
25 dynamics, we argue that dispersal syndromes can link trait-based ecology and meta-
26 ecosystem functioning together.

27 We highlight that the dispersal of individuals can be associated with functional effect traits
28 and can therefore alter trophic and nutrient-mediated interactions in ecosystems. We illustrate
29 how the association between dispersal tendency and functional traits can modify the spatial
30 heterogeneity of ecosystems.

31

32 **Abstract**

33 Dispersal mediates the flows of organisms in meta-communities and subsequently energy and
34 material flows in meta-ecosystems. Individuals within species often vary in dispersal
35 tendency depending on their phenotypic traits (i.e., dispersal syndromes), but the implications
36 of dispersal syndromes for meta-ecosystems have been rarely studied. Using empirical
37 examples on vertebrates, arthropods and microbes, we highlight that key functional traits can
38 be linked to dispersal. We argue that this coupling between dispersal and functional traits can
39 have consequences for meta-ecosystem functioning, mediating flows of functional traits and
40 thus the spatial heterogeneity of ecosystem functions. As dispersal syndromes may be
41 genetically determined, the spatial heterogeneity of functional traits may be further carried-
42 over across generations and link meta-ecosystem functioning to evolutionary dynamics.

43 **Keywords:** Dispersal syndrome, phenotypic variability, animal movement, ecosystem

44 functioning.

45

46 **Role of dispersal in meta-communities and meta-ecosystems**

47 The rise of **trait-based ecology** (see Glossary) has emphasised the importance of **individual**
48 **trait variability** for community structure and **ecosystem functioning** [1,2]. Key frameworks
49 have been elaborated to forecast ecosystem functioning from individual traits, such as the
50 metabolic theory of ecology and ecological stoichiometry [3,4]. Functional traits (particularly
51 **functional effect traits**, *sensu* [2]) indeed allow inferring causal mechanisms (e.g., body size
52 alters resource partitioning) that help understanding key ecosystem properties such as the
53 biodiversity-ecosystem functioning relationships. By determining biotic interactions in
54 communities, the variability of functional traits affects species coexistence and matter fluxes
55 (i.e. chemical elements, including nutrients) in food webs, ultimately altering ecosystem
56 processes [5].

57 Nonetheless, research on the effects of individual trait variability on ecosystems still
58 rarely considers the spatial structure of the environment [6–8]. Food webs in local
59 communities can indeed be connected by spatial flows of organisms forming a food web
60 **meta-community** [7]. **Dispersal** can affect biotic interactions (e.g., predation) in food web
61 meta-communities, modifying species coexistence within communities [9,10]. These
62 exchanges of organisms between local communities can modify nutrient fluxes within the
63 landscape that, added to abiotic energy and materials fluxes between and within local
64 ecosystems, form **meta-ecosystems**. Dispersal of organisms is a key process linking
65 populations and communities, and the resulting fluxes of nutrients sequestered in organisms
66 among habitats form a central part of meta-ecosystem dynamics as they affect primary
67 production, consumption and decomposition [11–13].

68 While dispersal was mostly considered as a rate in meta-community and meta-ecosystem
69 literature, it is now widely acknowledged to be a non-random process resulting from several
70 environmental factors, phenotypic traits and their interactions [14]. For instance, niche

71 breadth and life-history traits are correlated with dispersal variability among species [15].
72 Within species, dispersal decision of individuals can also depend upon their phenotype,
73 involving morphological, physiological or behavioural characteristics correlated with
74 dispersal. For instance, in rodents, dispersers are often more active, bolder and explore more
75 than residents [16]. Similarly, polymorphism (e.g. wing length of insects) is often associated
76 with dispersal distance [17]. Such correlation or co-occurrence between a suite of phenotypic
77 traits and dispersal forms a **dispersal syndrome** [14,16,18,19], that may result from multiple
78 ecological and evolutionary processes (Box 1).

79 Dispersal syndromes are known to affect the spatial heterogeneity of functional traits and
80 in turn mediate intra/interspecific interactions and meta-community dynamics [20–22].
81 However, whether this variability in the movements of organisms and their phenotypic traits
82 in landscapes can in turn modify the flows of energy and materials and affect food web meta-
83 community and meta-ecosystem functioning is rarely studied theoretically or empirically.
84 Here, we build upon empirical evidence on vertebrates, arthropods and microorganisms to
85 highlight that traits classically integrated into trait-based ecology and known for their role in
86 ecosystem functioning can be linked to dispersal propensity. Based on this evidence for
87 dispersal syndromes as a linkage between trait-based ecology and ecosystem functioning, we
88 point out potential implications of these dispersal syndromes for meta-ecosystem functioning
89 (Figure 1). We explore the consequences of dispersal syndromes and their evolution for the
90 spatial heterogeneity of ecosystem functions.

91

92 **On the ecosystem importance of dispersal-related traits**

93 The phenotypic structure of populations has received strong consideration from ecologists,
94 and the description of functional effect traits has allowed a mechanistic understanding of the
95 effects of individuals on ecosystems [2,23]. The variability of functional traits within a

96 species can be large [24], and can modify the strength of trophic and non-trophic interactions,
97 such as nutrient recycling within an ecosystem [25]. For example, consistent differences in
98 foraging behaviour in pale chubs (*Zacco platypus*) alter trophic cascades [26]; morphology of
99 mandible in shredders (*Gammarus fossarum*) drives decomposition rate [27]. Functional traits
100 and their intraspecific variability have hence consequences for species coexistence,
101 community structure, and subsequently drive the flows of energy and materials within and
102 among ecosystems.

103 Key functional traits have been found to be related to individual dispersal propensity:
104 in Table 1, we provide a list of relationships within the same species between dispersal and
105 phenotypic traits on the one hand, and between these phenotypic traits and functional effect
106 traits (sometimes even ecosystem functions) on the other hand. As such, in a freshwater fish
107 (*Salmo trutta*), higher dispersal propensities are associated with larger body sizes [28], a trait
108 correlated in this species with nutrient excretion rate [29] and known as key for ecosystem
109 functioning [30]. Moreover, movements of dispersers can be associated with higher metabolic
110 costs compared to residents [31] - metabolism is a key trait for ecosystem functioning [3] -
111 which can induce higher consumption rates to counterbalance the energetic expenditure (as
112 found in the butterfly *Melitaea cinxia*. [32,33]). Finally, dispersal is often part of a general
113 behavioural syndrome involving multiple behavioral traits [34]. In the signal crayfish
114 (*Pacifastacus leniusculus*), individuals staying in core populations (i.e., residents) of an
115 invasion front are more aggressive [35], which can alter multiple dimensions of ecosystems
116 such as trophic interactions in food webs [36,37].

117 Because of dispersal syndromes, individuals moving within a landscape can carry
118 different functional traits from individuals staying locally, and spatially heterogeneous
119 distribution of environmental conditions (e.g., environmental gradients, source-sink systems)
120 can make the fluxes of individual phenotypes asymmetric. Therefore, spatial variability of

121 functional traits can be generated among landscapes, potentially modifying the interactions
122 within meta-communities and in turn material and energy fluxes in meta-ecosystems. These
123 altered fluxes can affect two essential and intertwined dimensions of ecosystems: the strength
124 of **trophic interactions** and nutrient recycling. Especially, trophic interactions govern food
125 web structure in meta-communities, with subsequent effects on biomass production that are
126 key for meta-ecosystems functioning. First, dispersal syndromes can modify the spatial
127 heterogeneity of traits linked to energy and nutritional needs of organisms, consequently
128 modifying trophic interactions [3,36,38]. For instance, in decomposer species, dispersers may
129 display higher litter consumption, hence affecting the decomposition rate of organic matter,
130 although this effect varies among species [39]. In mosquitofish (*Gambusia affinis*), dispersers
131 are less sociable than residents, which affects prey biomass because sociability is correlated
132 with food intake [40]. Dispersal-related morphological traits can also be important for
133 ecosystem functioning. In pygmy grasshoppers (*Tetrix subatala*), a morphological
134 specialisation for dispersal (i.e., fully developed wings) is associated with a different diet
135 compared to wingless individuals [41]. This can potentially affect the recipient ecosystem
136 through altered trophic interactions. These examples show that dispersal syndromes can affect
137 material fluxes in food webs and thus ecosystem functions, such as decomposition of organic
138 matter, through changes in trophic interactions (Table 1) [42].

139 Second, dispersal syndromes can produce **nutrient-mediated effects**, modifying
140 nutrient and detritus influxes in ecosystems, both qualitatively and quantitatively [22]. In a
141 freshwater fish (*Salmo trutta*), larger individuals disperse farther than smaller individuals [28]
142 and display higher nutrient excretion rates (i.e., N and P) [29]. Such intraspecific variability in
143 nutrient excretion rate, resulting from catabolic and homeostatic mechanisms, is large enough
144 to generate functional differences among ecosystems, notably concerning primary production
145 [30,43]. Differences between residents and dispersers may affect the spatial variability of

146 productivity in meta-ecosystems. For example, in phosphorus-limited habitats, individuals
147 with a higher phosphorus excretion rate cause an increased biomass of primary producers
148 [44]. Organic material recycling might also be altered by differential mortality between
149 residents and dispersers induced by the costs of dispersal. For instance, dispersers can have a
150 higher parasite load than residents [45], which may increase mortality and thus alter the
151 stocks of dead organic matter. Moreover, the stoichiometry of organisms is an important
152 factor governing ecosystem functions [4], and has recently been discussed as a key parameter
153 linking dispersal to meta-ecosystems [22]. Intraspecific variability of stoichiometry has been
154 documented [4], and several studies suggest that differences between residents and dispersers
155 are likely. For instance, differences in chemical composition (e.g., lipid, triglyceride reserves)
156 between residents and dispersers have been found in marine fish [46] and insects [47]. Since
157 chemical compounds within organisms consist of different proportions of the basic elements,
158 differences in molecular traits (e.g., RNA content) and key physiological functions are
159 expected to be associated with variability in organisms' stoichiometry [48,49]. The potential
160 for dispersal syndromes to include stoichiometric variability might thus result in altered
161 nutrient flows among local ecosystems. Studying the three-way association between dispersal,
162 stoichiometry and ecosystem functioning is an important future challenge [22], especially
163 since dispersal can couple distant (but often similar) ecosystems, while resource flows mostly
164 occur locally [50].

165

166 **Implications of dispersal syndromes for meta-ecosystem functioning**

167 Meta-community research has emphasized the central role of dispersal as a process linking
168 biotic interactions, and global rates of material flows (through both abiotic and biotic fluxes)
169 among local ecosystems are core to meta-ecosystem theory [10,51]. However, dispersal can
170 be differentiated from abiotic fluxes as it can alter spatial distribution of organisms,

171 mediating directly biotic interactions, in addition to modify nutrient fluxes. For instance,
172 increasing dispersal rate tends to homogenize food webs and functions across space in a non-
173 linear manner, above a certain threshold [9,10,51] (though increasing consumer dispersal can
174 also generate spatial heterogeneity, e.g., [52]). Yet, dispersal is more than just movement rate
175 or distance, it also includes the phenotypic characteristics of resident and disperser
176 individuals, and therefore a potential different package of flowed nutrients (i.e., dispersing
177 individuals). However, the potential for differences between dispersers and residents in
178 multiple functional traits is currently not integrated in meta-ecosystem theory.

179 As highlighted above, dispersal syndromes often involve functional traits of major
180 importance for ecosystem functioning (Table 1). The heterogeneity of phenotypic
181 distributions resulting from dispersal syndromes, i.e., when dispersers have different
182 phenotypes than residents in heterogeneous landscapes, may thus generate spatial
183 differentiation in ecosystem functioning. For instance, the establishment of individuals or
184 species in novel habitats as occurring during recolonization or range shifts may be associated
185 with a non-random subset of traits, such as body mass or diet. This generates spatial
186 heterogeneity in functional trait distribution [53] and in turn affecting resource fluxes and thus
187 ecosystem biomass. Therefore, any biased flow of functional traits carried by dispersers in
188 heterogeneous landscapes may modify the spatial heterogeneity of meta-ecosystems, whose
189 importance could depend upon nutrient flows (Box 2).

190 The effects of dispersal on meta-ecosystems are known to depend on the rate of
191 dispersal in classic theory. With dispersal syndromes, since dispersers differ from residents,
192 differences in dispersal rate do not only change the total flow of organisms within meta-
193 ecosystems, but also mediate the spatial distribution of functional trait values (Box 2). For
194 instance, in a scenario where dispersers consume more resources than residents (as found in
195 [39]), intermediate dispersal rates would alter the heterogeneity of biomass consumption at

196 the meta-ecosystem scale compared to a scenario in which individuals disperse regardless of
197 their phenotype. Thus the heterogeneity in resource standing stock can be modified (Box 2).
198 Therefore, developing an integrative framework including dispersal syndromes in a meta-
199 ecosystem might benefit our understanding of spatially structured environments.

200 Importantly, dispersal syndromes can differ among populations or species [14–16].
201 Environmental conditions and evolutionary processes can strongly shape dispersal syndromes
202 [19]. The direction and the strength of covariations as well as the traits involved in dispersal
203 syndromes are the result of an evolutionary history where biotic interactions and landscape
204 configuration play a key role (e.g., [19,54], Box 1). The resulting variability in dispersal
205 syndromes and thus of flows of functional traits might alter meta-ecosystem dynamics
206 through trophic interactions and nutrient-mediated effects. For instance, when dispersal is
207 associated with high competitive abilities (e.g., due to higher aggressiveness as found in
208 bluebirds [55]), an increased dispersal rate would lead to an increase in competition strength
209 in colonized habitats. On the contrary, dispersers can often be poorer competitors (e.g.,
210 competition-colonisation trade-off, costs of dispersal, local exclusion of poorer competitors)
211 [31,56]. If competitive interactions drive community composition, the consequences of
212 dispersal for community composition, and subsequently the level and stability of ecosystem
213 functions are likely to depend on the form of dispersal syndromes and thus on their ecological
214 and evolutionary drivers.

215 The role of evolutionary processes for ecosystem functioning has been studied at the
216 local scale [23]. At the meta-community level, Urban & Skelly [57] have drawn a framework
217 integrating the evolution of intraspecific trait variation in meta-communities. They
218 emphasized that genetically based trait variation might be a major component of meta-
219 community structure affecting species coexistence. Therefore, by extending this concept,
220 dispersal syndromes can have two main roles in the evolutionary dynamics of meta-

221 communities and meta-ecosystems: eco-evolutionary dynamics and local adaptations. First,
222 since the evolution of intraspecific variability of dispersal and its associations with
223 phenotypic variability depend on biotic and abiotic conditions, the existence and form of
224 dispersal syndromes are likely to vary in space and time [19]. Therefore, eco-evolutionary
225 feedbacks between dispersal and meta-ecosystem functioning can arise because of
226 environmental fluctuations, due to the dependency of dispersal syndromes on abiotic
227 conditions and its effect on ecosystem functions. The consequences of dispersal for meta-
228 ecosystems are expected to differ depending on the nature of the syndrome (above and Box
229 2). Therefore, integrating the evolutionary dynamics of dispersal-related traits into meta-
230 ecosystem theories should help understand how ecosystem functioning varies in the face of
231 environmental changes.

232 Second, dispersal is generally expected to slow down adaptation by homogenizing
233 local gene pools, at least over a certain threshold. Nonetheless, theoretical and experimental
234 studies showed that it may instead promote local adaptation and thus population phenotypic
235 differentiation when individuals choose to disperse and settle in habitats that better suit their
236 phenotype [58]. Since dispersal syndromes are also expected to generate spatial heterogeneity
237 of phenotypic traits, the interaction between dispersal syndromes and habitat choice might
238 alter the dynamics of trait variation within and between populations. Whether dispersal
239 syndromes are fixed at the scale of population or species or depend on environmental
240 conditions (Box 1) might generate dynamic phenotypic flows in meta-ecosystems according
241 to evolutionary dynamics (e.g., local adaptation) and ecological context. By modifying trait
242 dynamics within and among populations, dispersal syndromes might hence alter functional
243 divergences among food webs and ecosystems across generations. Indeed, functional traits
244 linked to dispersal propensity may be inherited across generations and so may be the
245 consequences of these traits for ecosystem functioning [59]. Investigating the potential for

246 such eco-evolutionary dynamics of dispersal to affect biotic interactions and as a result food
247 webs and ecosystems is of particular importance.

248

249 **Concluding remarks**

250 Dispersal syndromes mediate phenotypic distributions and hence interaction strength
251 and nutrient release in ecological networks and thus may play a major role in meta-ecosystem
252 functioning. We especially pointed out that links between dispersal and traits of key
253 importance for ecosystem functioning can modify trophic interactions and material fluxes. For
254 example, dispersal syndromes can make dispersal increase spatial heterogeneity in ecosystem
255 functioning relative to cases without dispersal syndromes. Predictions regarding spatial
256 dynamics of meta-ecosystems may hence benefit from the integration of dispersal syndromes.
257 Yet, dispersal syndromes can greatly vary across species in both direction and traits involved,
258 which might affect the consequences for meta-ecosystems as illustrated in Box 2. Improving
259 our understanding of the role of dispersal for the spatial dynamics of meta-ecosystems will
260 thus require further effort in integrating dispersal syndromes in meta-ecosystem theoretical
261 frameworks, but also increased investigation of the ecological and evolutionary drivers of
262 dispersal syndromes.

263 Modelling approaches can be a powerful method to evaluate the role of phenotypic-
264 dependent dispersal for meta-ecosystem functioning. For instance, existing models (see for
265 example [22,52]) can be modified to implement dispersal syndromes. It would allow to
266 determine whether the phenotypic differences between dispersing and non-dispersing
267 individuals might result in an increased complexity in ecological interactions, potentially
268 quantitatively or qualitatively altering meta-ecosystems functioning and stability (e.g., [60]).
269 Such models should further allow assessing whether and how the evolution of dispersal
270 syndromes alter meta-ecosystem dynamics. The evolution of dispersal syndromes is important

271 to account for since anthropogenic pressures change the environmental conditions that are
272 known to shape dispersal syndromes (e.g., habitat fragmentation).

273 Transposing those predictions to nature is challenging due to the inherent large scale
274 of meta-ecosystem frameworks [8], but correlative approaches in the field coupled with
275 adequate statistics (e.g., structural equation modelling) can bring insights on the relationships
276 between dispersal syndromes, spatially structured diversity and ecosystem patterns. A further
277 necessary step to identify whether dispersal syndromes directly or indirectly affect meta-
278 ecosystems will be to take advantage of the increasingly used micro/mesocosm experiments.
279 Manipulating dispersal syndromes (i.e., shape and variance) and key characteristics of the
280 environment (e.g., abiotic conditions, habitat fragmentation) in simplified meta-ecosystems is
281 an essential step forward for our comprehension of the effects of dispersal syndromes on
282 biodiversity, biomass production and stability of meta-ecosystems. Understanding the role of
283 variability of dispersal for meta-ecosystem functioning is an exciting and challenging topic
284 for years to come (see Outstanding Questions). In a world where human activities are
285 constantly shaping landscape structure, considering those issues might also help design
286 ecological applications, such as conservation strategies.

287

288 **Acknowledgements**

289 AR is supported by a F.R.S.-FNRS research project (PDR T.0211.19) awarded to NS in
290 collaboration with SJ. NS is Senior Research Associate of the F.R.S.-FNRS and supported by
291 an Action de Recherche Concertée grant (ARC 18/23-095). SJ, EB, BH and JC are part of
292 TULIP (Laboratory of Excellence Grant ANR-10 LABX-41), SJ is supported by the Agence
293 Nationale de la Recherche for the project CHOOSE (ANR-19-CE02-0016), and JC by the
294 European Research Council (ERC) under the European Union's Horizon 2020 research and

295 innovation programme (grant agreement No 817779). This paper is contribution BRCXXX of
296 the Biodiversity Research Center at UCLouvain.

297

298 **References**

- 299 1 McGill, B. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol.*
300 *Evol.* 21, 178–185
- 301 2 Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
- 302 3 Brown, J.H. *et al.* (2004) Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789
- 303 4 Leal, M.C. *et al.* (2016) The ecology and evolution of stoichiometric phenotypes. *Trends*
304 *Ecol. Evol.* DOI: 10.1016/j.tree.2016.11.006
- 305 5 Díaz, S. *et al.* (2013) Functional traits, the phylogeny of function, and ecosystem service
306 vulnerability. *Ecol. Evol.* 3, 2958–2975
- 307 6 Loreau, M. *et al.* (2003) Meta-ecosystems: a theoretical framework for a spatial
308 ecosystem ecology. *Ecol. Lett.* 6, 673–679
- 309 7 Massol, F. *et al.* (2011) Linking community and ecosystem dynamics through spatial
310 ecology: An integrative approach to spatial food webs. *Ecol. Lett.* 14, 313–323
- 311 8 Gonzalez, A. *et al.* (2020) Scaling-up biodiversity-ecosystem functioning research. *Ecol.*
312 *Lett.* 23, 757–776
- 313 9 Loreau, M. *et al.* (2003) Biodiversity as spatial insurance in heterogeneous landscapes.
314 *Proc. Natl. Acad. Sci.* 100, 12765–12770
- 315 10 Thompson, P.L. and Gonzalez, A. (2017) Dispersal governs the reorganization of
316 ecological networks under environmental change. *Nat. Ecol. Evol.* 1, 0162
- 317 11 Lundberg, J. and Moberg, F. (2003) Mobile link organisms and ecosystem functioning:
318 implications for ecosystem resilience and management. *Ecosystems* 6, 0087–0098
- 319 12 Gravel, D. *et al.* (2010) Source and sink dynamics in meta-ecosystems. *Ecology* 91, 2172–
320 2184
- 321 13 Gravel, D. *et al.* (2010) Patch dynamics, persistence, and species coexistence in
322 metaecosystems. *Am. Nat.* 176, 289–302
- 323 14 Clobert, J. *et al.* (2009) Informed dispersal, heterogeneity in animal dispersal syndromes
324 and the dynamics of spatially structured populations. *Ecol. Lett.* 12, 197–209
- 325 15 Stevens, V.M. *et al.* (2014) A comparative analysis of dispersal syndromes in terrestrial
326 and semi-terrestrial animals. *Ecol. Lett.* 17, 1039–1052
- 327 16 Le Galliard, J.-F. *et al.* (2012) Patterns and processes of dispersal behaviour in arvicoline
328 rodents: dispersal mechanisms in microtine rodents. *Mol. Ecol.* 21, 505–523
- 329 17 Zera, A.J. and Denno, R.F. (1997) Physiology and ecology of dispersal polymorphism in
330 insects. *Annu. Rev. Entomol.* 42, 207–230
- 331 18 Sih, A. *et al.* (2004) Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* 79, 241–
332 277
- 333 19 Cote, J. *et al.* (2017) Evolution of dispersal strategies and dispersal syndromes in
334 fragmented landscapes. *Ecography* 40, 56–73
- 335 20 Jacob, S. *et al.* (2015) Habitat matching and spatial heterogeneity of phenotypes:
336 implications for metapopulation and metacommunity functioning. *Evol. Ecol.* 29, 851–
337 871

- 338 21 Jacob, S. *et al.* (2019) Variability in dispersal syndromes is a key driver of metapopulation
339 dynamics in experimental microcosms. *Am. Nat.* 194, 613–626
- 340 22 Massol, F. *et al.* (2017) How life-history traits affect ecosystem properties: effects of
341 dispersal in meta-ecosystems. *Oikos* 126, 532–546
- 342 23 Matthews, B. *et al.* (2011) Toward an integration of evolutionary biology and ecosystem
343 science. *Ecol. Lett.* 14, 690–701
- 344 24 Siefert, A. *et al.* (2015) A global meta-analysis of the relative extent of intraspecific trait
345 variation in plant communities. *Ecol. Lett.* 18, 1406–1419
- 346 25 Raffard, A. *et al.* (2019) The community and ecosystem consequences of intraspecific
347 diversity: a meta-analysis. *Biol. Rev.* 94, 648–661
- 348 26 Katano, O. (2011) Effects of individual differences in foraging of pale chub on algal
349 biomass through trophic cascades. *Environ. Biol. Fishes* 92, 101–112
- 350 27 Rota, T. *et al.* (2018) Phenotypic determinants of inter-individual variability of litter
351 consumption rate in a detritivore population. *Oikos* 127, 1670–1678
- 352 28 Vøllestad, L.A. *et al.* (2012) Small-scale dispersal and population structure in stream-
353 living brown trout (*Salmo trutta*) inferred by mark–recapture, pedigree reconstruction,
354 and population genetics. *Can. J. Fish. Aquat. Sci.* 69, 1513–1524
- 355 29 Villéger, S. *et al.* (2012) Intra- and interspecific differences in nutrient recycling by
356 European freshwater fish. *Freshw. Biol.* 57, 2330–2341
- 357 30 Schmitz, O.J. *et al.* (2010) Predator control of ecosystem nutrient dynamics. *Ecol. Lett.*
358 13, 1199–1209
- 359 31 Bonte, D. *et al.* (2012) Costs of dispersal. *Biol. Rev.* 87, 290–312
- 360 32 Niitepõld, K. *et al.* (2009) Flight metabolic rate and *Pgi* genotype influence butterfly
361 dispersal rate in the field. *Ecology* 90, 2223–2232
- 362 33 Niitepõld, K. (2019) Effects of flight and food stress on energetics, reproduction, and
363 lifespan in the butterfly *Melitaea cinxia*. *Oecologia* 191, 271–283
- 364 34 Reale, D. *et al.* (2010) Personality and the emergence of the pace-of-life syndrome
365 concept at the population level. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 4051–4063
- 366 35 Hudina, S. *et al.* (2015) Differences in aggressive behaviour along the expanding range of
367 an invasive crayfish: an important component of invasion dynamics. *Biol. Invasions* 17,
368 3101–3112
- 369 36 Toscano, B.J. *et al.* (2016) Personality, foraging behavior and specialization: integrating
370 behavioral and food web ecology at the individual level. *Oecologia* 182, 55–69
- 371 37 Pintor, L.M. *et al.* (2009) Behavioral correlations provide a mechanism for explaining high
372 invader densities and increased impacts on native prey. *Ecology* 90, 581–587
- 373 38 McCauley, S.J. *et al.* (2010) Foraging rates of larval dragonfly colonists are positively
374 related to habitat isolation: results from a landscape-level experiment. *Am. Nat.* 175,
375 E66–E73
- 376 39 Little, C.J. *et al.* (2019) Dispersal syndromes can impact ecosystem functioning in
377 spatially structured freshwater populations. *Biol. Lett.* 15, 20180865
- 378 40 Cote, J. *et al.* (2017) Non-random dispersal mediates invader impacts on the
379 invertebrate community. *J. Anim. Ecol.* 86, 1298–1307
- 380 41 Karpestam, E. and Forsman, A. (2013) Stable isotopes reveal dietary divergence between
381 dispersal phenotypes in *Tetrix subulata* pygmy grasshoppers (Orthoptera: Tetrigidae).
382 *Eur. J. Entomol.* 110, 65–70
- 383 42 Schmid, D.W. *et al.* (2019) Rapid divergence of predator functional traits affects prey
384 composition in aquatic communities. *Am. Nat.* 193, 331–345

- 385 43 Bassar, R.D. *et al.* (2010) Local adaptation in Trinidadian guppies alters ecosystem
386 processes. *Proc. Natl. Acad. Sci.* 107, 3616–3621
- 387 44 Evangelista, C. *et al.* (2017) Resource composition mediates the effects of intraspecific
388 variability in nutrient recycling on ecosystem processes. *Oikos* 126, 1439–1450
- 389 45 Clobert, J. *et al.* (2001) *Dispersal*, Oxford University Press.
- 390 46 Shima, J.S. *et al.* (2015) Consequences of variable larval dispersal pathways and resulting
391 phenotypic mixtures to the dynamics of marine metapopulations. *Biol. Lett.* 11,
392 20140778
- 393 47 Zera, A.J. *et al.* (1994) Lipid, carbohydrate and nitrogen content of long- and short-
394 winged *Gryllus firmus*: Implications for the physiological cost of flight capability. *J. Insect*
395 *Physiol.* 40, 1037–1044
- 396 48 Gillooly, J.F. *et al.* (2005) The metabolic basis of whole-organism RNA and phosphorus
397 content. *Proc. Natl. Acad. Sci.* 102, 11923–11927
- 398 49 Jeyasingh, P.D. and Weider, L.J. (2007) Fundamental links between genes and elements:
399 evolutionary implications of ecological stoichiometry. *Mol. Ecol.* 16, 4649–4661
- 400 50 Gounand, I. *et al.* (2018) Meta-ecosystems 2.0: rooting the theory into the field. *Trends*
401 *Ecol. Evol.* 33, 36–46
- 402 51 Thompson, P.L. *et al.* (2020) A process-based metacommunity framework linking local
403 and regional scale community ecology. *Ecol. Lett.* 23, 1314–1329
- 404 52 Gounand, I. *et al.* (2014) The Paradox of Enrichment in Metaecosystems. *Am. Nat.* 184,
405 752–763
- 406 53 Messenger, M.L. and Olden, J.D. (2019) Phenotypic variability of rusty crayfish (*Faxonius*
407 *rusticus*) at the leading edge of its riverine invasion. *Freshw. Biol.* 64, 1196–1209
- 408 54 Legrand, D. *et al.* (2015) Ranking the ecological causes of dispersal in a butterfly.
409 *Ecography* 38, 822–831
- 410 55 Duckworth, R.A. and Badyaev, A.V. (2007) Coupling of dispersal and aggression facilitates
411 the rapid range expansion of a passerine bird. *Proc. Natl. Acad. Sci.* 104, 15017–15022
- 412 56 Cadotte, M.W. *et al.* (2006) On testing the competition-colonization trade-off in a
413 multispecies assemblage. *Am. Nat.* 168, 704–709
- 414 57 Urban, M.C. and Skelly, D.K. (2006) Evolving metacommunities: toward an evolutionary
415 perspective on metacommunities. *Ecology* 87, 1616–1626
- 416 58 Edelaar, P. *et al.* (2008) Matching habitat choice causes directed gene flow: a neglected
417 dimension in evolution and ecology. *Evolution* 62, 2462–2472
- 418 59 Whitham, T.G. *et al.* (2006) A framework for community and ecosystem genetics: from
419 genes to ecosystems. *Nat. Rev. Genet.* 7, 510–523
- 420 60 Gravel, D. *et al.* (2016) Stability and complexity in model meta-ecosystems. *Nat.*
421 *Commun.* 7, 12457
- 422 61 Berggren, H. *et al.* (2012) Spatial sorting may explain evolutionary dynamics of wing
423 polymorphism in pygmy grasshoppers. *J. Evol. Biol.* 25, 2126–2138
- 424 62 Cucherousset, J. *et al.* (2007) Stable isotope evidence of trophic interactions between
425 introduced brook trout *Salvelinus fontinalis* and native brown trout *Salmo trutta* in a
426 mountain stream of south-west France. *J. Fish Biol.* 71, 210–223
- 427 63 Bolnick, D.I. *et al.* (2009) Phenotype-dependent native habitat preference facilitates
428 divergence between parapatric lake and stream stickleback. *Evolution* 63, 2004–2016
- 429 64 Matthews, B. *et al.* (2016) Experimental evidence of an eco-evolutionary feedback
430 during adaptive divergence. *Curr. Biol.* 26, 483–489

- 431 65 Dingemanse, N.J. *et al.* (2003) Natal dispersal and personalities in great tits (*Parus major*
432). *Proc. R. Soc. Lond. B Biol. Sci.* 270, 741–747
- 433 66 Dingemanse, N.J. and de Goede, P. (2004) The relation between dominance and
434 exploratory behavior is context-dependent in wild great tits. *Behav. Ecol.* 15, 1023–1030
- 435 67 Ebenhard, T. (1987) High activity in bank voles in relation to colonization ability. *Oikos*
436 49, 297
- 437 68 Zera, A.J. and Zhao, Z. (2006) Intermediary metabolism and life-history trade-offs:
438 differential metabolism of amino acids underlies the dispersal-reproduction trade-off in
439 a wing-polymorphic cricket. *Am. Nat.* 167, 889–900
- 440 69 De Fraipont, M. *et al.* (2000) Increased pre-natal maternal corticosterone promotes
441 philopatry of offspring in common lizards *Lacerta vivipara*. *J. Anim. Ecol.* 69, 404–413
- 442 70 Meylan, S. *et al.* (2002) Stress and body condition as prenatal and postnatal
443 determinants of dispersal in the common lizard (*Lacerta vivipara*). *Horm. Behav.* 42,
444 319–326
- 445 71 Cote, J. *et al.* (2006) Experimental enhancement of corticosterone levels positively
446 affects subsequent male survival. *Horm. Behav.* 49, 320–327
- 447 72 Cote, J. *et al.* (2010) Food deprivation modifies corticosterone-dependent behavioural
448 shifts in the common lizard. *Gen. Comp. Endocrinol.* 166, 142–151
- 449 73 Shine, R. *et al.* (2011) An evolutionary process that assembles phenotypes through space
450 rather than through time. *Proc. Natl. Acad. Sci.* 108, 5708–5711
- 451 74 Jacob, S. and Legrand, D. (2021) Phenotypic plasticity can reverse the relative extent of
452 intra- and interspecific variability across a thermal gradient. *Proc. R. Soc. B Biol. Sci.* 288,
453 20210428
- 454

455 **Glossary**

456 **Dispersal:** Any movement of individuals from one population to another that can potentially lead to gene
457 flow. Dispersal must not be confounded with migration, i.e., a back-and-forth movement (often seasonal
458 but not only) between a reproduction site and a site where other parts of the life cycle are spent.

459 **Dispersal syndrome:** Suite of phenotypic traits correlated with dispersal (i.e., differentiating dispersers
460 from residents or along dispersal rate or distance).

461 **Ecosystem functioning:** Set of processes (or functions) describing changes in energy and matter dynamics
462 due to biological, physical or geochemical factors.

463 **Functional effect trait:** Individual characteristics affecting community or ecosystem processes (also
464 referred to as functional traits in the text). Can be differentiated from functional response traits allowing
465 organisms to cope with environmental variability.

466 **Individual trait variability** (= intraspecific trait variability): Variability of trophic, physiological,
467 behavioral or morphological features displayed by individuals within a species.

468 **Meta-community:** Set of local communities linked by the dispersal of organisms. Multiple theoretical
469 meta-communities have been studied, such as food web meta-communities or competitive meta-
470 communities.

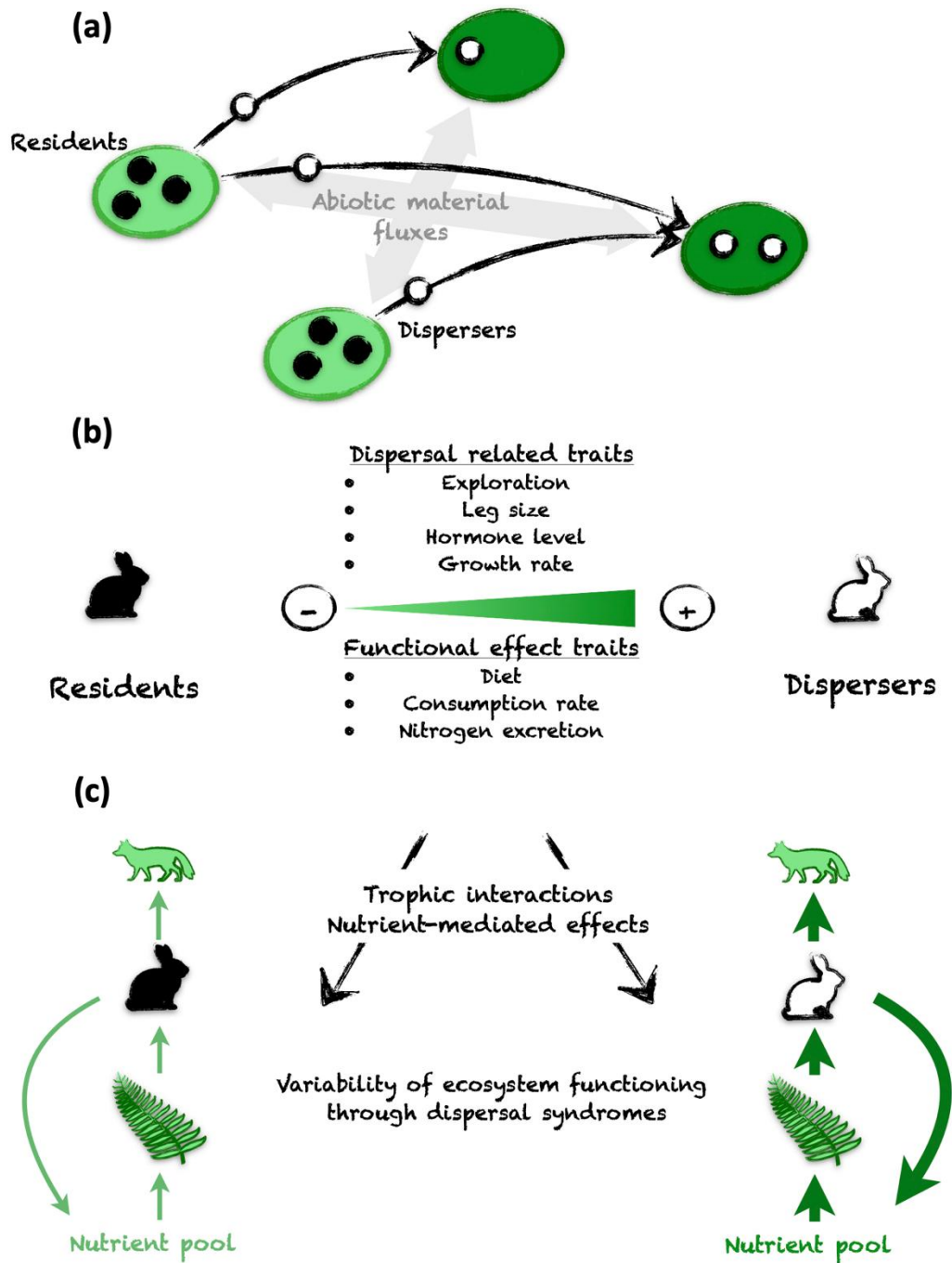
471 **Meta-ecosystem:** Set of local ecosystems connected by flows of energy, matter, and organisms.

472 **Nutrient-mediated effects:** Modification of the dynamics of nutrient elements independently of
473 consumptive effects, for instance through excretion of nitrogen, phosphorus, or carbon.

474 **Trait-based ecology:** Study of the interactions between organisms' phenotype and their environment.

475 **Trophic interactions:** Interactions linked to the feeding habits and the consumption of organisms and
476 describing vertical matter fluxes.

477



478
 479
 480
 481
 482
 483
 484
 485
 486
 487
 488
 489
 490

Figure 1. Overview of the potential linkage between dispersal syndromes and meta-ecosystem functioning through covariations with functional effect traits. (a) Dispersal syndromes consist of dispersers (white circles) with different phenotypes than residents (black circles), potentially leading to a spatial heterogeneity in the distribution of phenotypic traits. Grey arrows represent abiotic fluxes (nutrients and material) which may interact with dispersal in shaping meta-ecosystem functioning. (b) Dispersal syndromes can involve multiple phenotypic traits, such as morphology (e.g., leg size) or physiology (e.g., hormones levels). These traits are known to be linked to key functional effect traits important for ecosystem functions such as consumption rate, nitrogen excretion, and nutrient recycling. The figure illustrates an example where dispersers are more active explorers and consume more resource than residents, but other relationships can exist (Table 1). (c) Dispersal syndromes can therefore make local ecosystems differ in key properties such as biomass production,

491 consumption rate, and nutrient recycling, hence increasing spatial heterogeneity of meta-
492 ecosystem functioning.
493
494

495 **Table 1. Traits involved in dispersal syndromes are often linked with functional traits of**
496 **key importance for ecosystem dynamics.** We draw a non-exhaustive list of empirical
497 examples where a trait in a given species is involved in dispersal syndromes and where the
498 same trait (or dispersal directly) is linked to a functional effect trait, therefore potentially
499 sustaining dispersal syndrome effects on meta-ecosystems. Positive and negative correlations
500 are denoted by a (-) and a (+), respectively.

Trait category	Species	Dispersal-related traits	Functional effect traits	Expected relationship between dispersal and functional effect trait
Morphology	Pygmy grasshopper (<i>Tetrix subulate</i> , arthropod)	Wing length (+) [17,61]	Diet (+) [41]	Dispersal is positively correlated with trophic position
	Brown trout (<i>Salmo trutta</i> , fish)	Body length (-) [28]	Diet/ Excretion rate (+) [62][29]	Dispersal is negatively correlated with N-excretion rate and trophic position
	Threespine stickleback (<i>Gasterosteus aculeatus</i> , fish)	Stream morphology (+) [63]	Prey biomass (-) [64]	Dispersal reduces prey biomass
Behaviour	Mosquitofish (<i>Gambusia affinis</i> , fish)	Sociability (-) [40]	Prey biomass (+) [40]	Dispersal reduces prey density
	Signal crayfish (<i>Pasifastacus lenisculus</i> , arthropod)	Aggressiveness (-) [35]	Food consumption (+) [37]	Dispersal is negatively correlated with prey consumption
	Great tit (<i>Parus major</i> , bird)	Exploration (+) [65]	Competitive dominance (+) [66]	Dispersal is positively correlated with competitiveness
	Bank vole (<i>Myodes glareolus</i> , mammal)	Activity (+) [67]	Food consumption (+) [67]	Dispersal is positively correlated with consumption rate
	Dragonfly (<i>Libellula spp.</i> , arthropod)	Colonization distance (+) [38]	Food consumption (+) [38]	Dispersal is positively correlated with consumption rate
Physiology	Sand field cricket (<i>Gryllus firmus</i> , arthropod)	Lipid and amino acid metabolism (+) [17,68]	Nutrient content (+) [47]	Dispersal is positively correlated with lipid and triglyceride content
	Common lizard (<i>Lacerta vivipara</i> , squamate)	Corticosterone (-) [69,70]	Food consumption (+) [71,72]	Dispersal is negatively correlated with food intake
	Glanville fritillary (<i>Melitaea cinxia</i> , arthropod)	Metabolic rate (+) [32]	Food consumption (+) [33]	Dispersal is positively correlated with food intake
Life history	Common triplefin (<i>Forsterygion lapillum</i> , fish)	Growth rate (-) [46]	Nutrient content (-) [46]	Dispersal is negatively correlated with lipid concentration

501
502

Box 1. Processes generating dispersal syndromes and their consequences for meta-ecosystems.

Dispersal is part of large association among suites of phenotypic traits (e.g., pace-of-life framework [34]) whose respective evolution can greatly influence each other. Multiple processes can explain these covariations between phenotype and dispersal [14,19,22], which may generate variability of dispersal syndromes within and between species. First, trade-offs may result in negative correlations between dispersal and other traits, as when allocation of time and energy to dispersal limits investment in other biological functions (e.g., foraging, immunity). Second, syndromes can emerge from structural links between dispersal and other traits, including gene pleiotropy or allometric scaling. Finally, dispersal syndromes can result from selection, when the environment favors both dispersal and other traits (co-selection) or when selection on dispersal affects the evolution of other traits or the reverse (joint-selection). In addition, both dispersal and related phenotypic traits can be determined by both genetic and environmental factors [19], which can generate different levels of spatial and temporal variability in dispersal syndromes. The level of heritability of traits involved in dispersal syndromes can modify the strength, direction, and variance of correlations between traits and dispersal across generations. Furthermore, plasticity in dispersal and related traits along environmental conditions can result in important and rapid changes in traits and their covariations, potentially generating high variability in dispersal syndromes.

Depending on the relative importance of processes generating dispersal syndromes and their variation across time and space, the extent of intraspecific variation and direction of correlations between dispersal and functional traits might change among localities. Investigating how much dispersal syndromes vary among localities is thus crucial to better understand their importance for example on meta-population dynamics [21], species range distribution [73], or the diversity and stability of meta-ecosystems [60]. For instance, landscape fragmentation usually increases dispersal costs and might exacerbate dispersal syndromes that result from trade-offs [19], ultimately potentially increasing the consequences for the spatial heterogeneity of meta-ecosystems. Furthermore, environmental changes can generate different levels of intra- and interspecific variability of dispersal syndromes when dispersal and related traits are plastic [74]. We might expect the resulting variability of dispersal syndromes to determine the strength and type of species interactions, thereby modifying patterns of diversity within communities and potentially meta-ecosystem stability and resilience. Identifying which mechanisms underlie variability of dispersal syndromes is thus one of the key challenges to better understand their effects on meta-ecosystem functioning.

503

504

Box 2. A mathematical illustration of the potential effects of dispersal syndromes on a key component of meta-ecosystems: consumption rate.

We investigated the consequences of dispersal for the spatial variability of consumption rate, a key component of meta-ecosystems, when dispersal is correlated positively or negatively to this functional trait, as found in many species (see for instance Table 1). To do so, we constructed a meta-population model with dispersal of a consumer in a landscape consisting of a 10-habitat patch network. Local environmental conditions varied randomly and temporally, leading to random local extinctions. We drew multiple scenarios involving dispersal syndromes (see Supplementary information). In a scenario of absence of a dispersal syndrome (i.e., residents and dispersers display equal consumption rates; yellow lines), increasing dispersal rate is expected to increase total resource consumption (left panel), and decrease its spatial heterogeneity (non-linearly; right panel) in meta-ecosystems. We then considered dispersal syndromes, with dispersers showing either higher (competitive advantage) or lower (competition-colonization trade-off) consumption rate compared to residents, while setting the mean consumption rate constant across different dispersal probabilities. In the case of a positive association of consumption rate and dispersal (blue lines), we observed a slight increase in total resource consumption at intermediate dispersal rates (Figure 1a), resulting from increased abundance of the disperser phenotype following recolonization of extinct patches. Although the effects on resource consumption at the landscape scale (left panel) are weak, they create an important spatial heterogeneity of resource consumption in the meta-ecosystem (Figure 1b). While increasing dispersal always has a homogenizing effect above a certain threshold, the inclusion of a dispersal syndrome where dispersers are weaker consumers than residents (red curve) could strongly moderate this effect resulting in higher heterogeneity than previously predicted. On the contrary, higher consumption in dispersers (blue curve) results in a decrease of spatial heterogeneity of ecosystem function and alleviates the effect of dispersal rate. The integration of abiotic nutrient fluxes will be an important next step since they may affect species persistence and interactions. Therefore, further studies should investigate whether abiotic fluxes interact with or blur the effects of dispersal syndromes on local biomass and nutrient recycling. This simple model highlights the potential for dispersal syndromes to significantly affect the spatial variability in ecosystem function, with direction of effects that depends on the type of dispersal syndrome considered, pointing out the potential for further investigation of the integration of dispersal syndromes in meta-ecosystem theory.

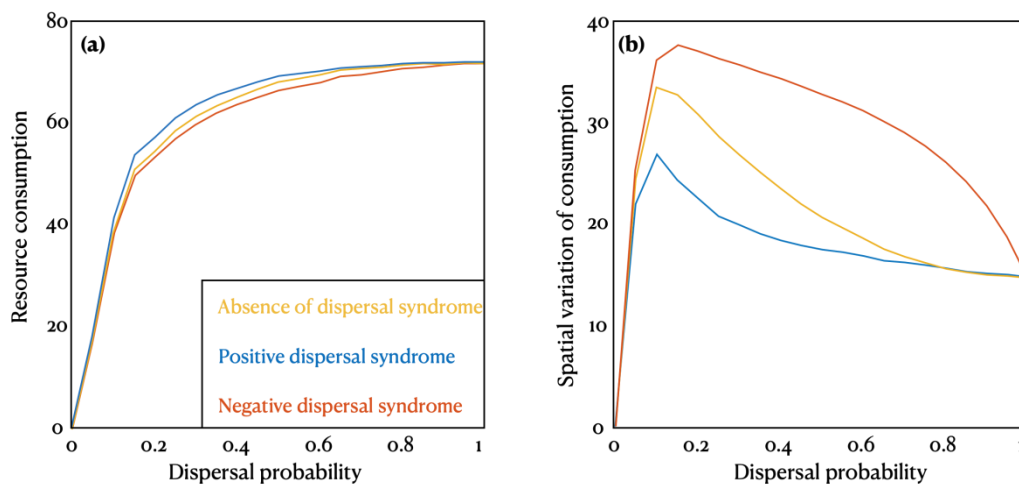


Figure 1. Hypothetical examples of consequences of dispersal syndromes for resource consumption in the meta-ecosystem, concerning both its average value (a) and its spatial heterogeneity of resource consumption (b).

505 **Outstanding questions.**

506 Can landscape configuration and anthropogenic modifications of landscapes (e.g.
507 fragmentation) mediate dispersal syndromes effects on meta-ecosystems? How do different
508 regimes of spatial and temporal variability in environmental conditions affect dispersal
509 syndromes and their ecosystem consequences?

510 Marine, freshwater and terrestrial ecosystems often differ in their environmental variability
511 and constrains on dispersal movements. Do the evolution of dispersal syndromes and
512 consequences for meta-ecosystems differ across biomes?

513 In what ways do the mechanisms underlying dispersal syndromes (plastic or genetic)
514 determine the nature and timing of meta-ecosystem consequences? Do meta-ecosystem
515 dynamics affect in turn the evolution of dispersal syndromes? Do eco-evolutionary feedbacks
516 between dispersal syndromes evolution and ecosystem dynamics exist and how do they drive
517 long-term dynamics of ecosystem functioning?

518 How do differences of mechanisms underlying syndromes and the relative importance of
519 intra- and inter-specific variability affect meta-ecosystem dynamics? How to integrate such
520 variability within and among species in meta-ecosystem theoretical framework?

521 Invasion dynamics and range expansions of populations are currently occurring worldwide.
522 Does integration of dispersal syndromes in these theories help predict future impacts on
523 ecosystems?

524 How to decipher the effects of population density from that of phenotypic differentiation in
525 natural systems?

526 May dispersal syndromes change qualitatively or quantitatively the effects of dispersal for
527 spatial and temporal stability (including resilience and resistance) of meta-ecosystems?

528 What are the species characteristics (trophic level, functional role, passive or active dispersal,
529 dispersal distance) that make dispersal syndrome more or less important at the meta-
530 community and meta-ecosystem scales?

531

532 **Supplementary information**

533 Model description (Box 2)

534 We model a meta-population consisting of $M = 10$ identical patches. Each patch can maintain
535 a population of $K = 100$ individuals. The populations are composed of two types of
536 individuals, residents and dispersers, which can differ in their resource consumption. In the
537 case of a positive (negative) dispersal syndrome, dispersers consume more (less) resource
538 than residents, while in the absence of a dispersal syndrome, dispersers and residents consume
539 the same amount of resource.

540 We subject this meta-population to a random sequence of local extinctions, with $p_E =$
541 0.2 the extinction probability per patch and per generation. We study the response of the
542 meta-population to these perturbations, in particular the spatial (and temporal) variation of
543 resource consumption per patch. We are interested in how these quantities depend on the
544 dispersal probability p_D (i.e., the fraction of dispersers) and on the type of dispersal syndrome
545 (no syndrome, positive and negative).

546 When varying dispersal probability p_D , we keep constant the mean resource
547 consumption per individual. That is, denoting by c_D and c_R the resource consumption of a
548 disperser and a resident, respectively, we keep $p_D c_D + (1 - p_D) c_R = 1$ when varying p_D . The
549 type of dispersal syndrome determines the ratio c_D / c_R (1, 5 or 1/5 for no, positive and
550 negative syndrome, respectively), so that we get

551

$$c_D = c_R = 1 \quad \text{for no dispersal syndrome}$$

$$c_D = 5 c_R = \frac{1}{p_D + \frac{1-p_D}{5}} \quad \text{for a positive dispersal syndrome}$$

$$c_D = \frac{1}{5} c_R = \frac{1}{p_D + 5(1-p_D)} \quad \text{for a negative dispersal syndrome}$$

552

553 Then, for a set of parameter values p_D , c_D and c_R , the simulations proceed as follows:

554 Initially all patches are occupied by $K/2 = 50$ individuals.

555 1. Some of the patches become extinct. For each patch an extinction occurs with
556 probability $p_E = 0.2$. This means that a patch undergoes extinction on average every
557 five generations.

558 2. For each individual the dispersal phenotype is determined with probability p_D a
559 disperser, or else a resident. Then the dispersers redistribute over the meta-
560 population. The dispersal process is assumed to be spatially uniform: for each
561 disperser its new patch is randomly drawn from the set of $M = 10$ patches.

562 3. Individuals reproduce in a density-dependent way. For each parent the number of
563 off- spring is Poisson distributed with mean $\frac{2K}{K+N}$, where N is the number of
564 individuals (both dispersers and residents) in the patch. After reproduction the
565 parent individuals die. Hence, the new number of individuals in the patch is on
566 average $N \frac{2K}{K+N}$. This formula implies that the population is expected to double for a
567 small population ($N \ll K$) and to remain constant for a population close to carrying
568 capacity $K = 100$, as it should.

569 After this last step the simulation continues at step 1 for the next generation.

570 The resource consumption of an individual is assumed to be proportional to its number
571 of offspring. Hence, denoting by N_D and N_R the number of offspring produced in a patch by
572 dispersers and residents, respectively, the total resource consumption in that patch is given by
573 $c_D N_D + c_R N_R$. Note that resource consumption does not affect the meta-population dynamics,
574 so that the same simulations can be used to study different combinations c_D and c_R (i.e.,
575 different types of dispersal syndrome).

576 In each simulation we monitor the resource consumption during 1000 generations.

577 Using these monitored values ($M = 10$ patches \times 1000 generations), we compute the (spatio-

578 temporal) mean resource consumption per patch and the (temporal) mean standard deviation
579 of resource consumption between patches. We obtain similar results when considering the
580 temporal rather than spatial variation of resource consumption. We repeat this procedure 10
581 times for each value of dispersal probability p_D ranging from 0 to 1 in steps of 0.05. The
582 figure of Box 2 shows results averaged over the 10 replicates.
583