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1 HOW LIFE-HISTORY TRAITS AFFECT ECOSYSTEM PROPERTIES: 2 EFFECTS OF DISPERSAL IN META-ECOSYSTEMS

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17 18 **ABSTRACT**

19 The concept of life-history traits and the study of these traits are the hallmark of population
20 biology. Acknowledging their variability and evolution has allowed us to understand how species
21 adapt in response to their environment. The same traits are also involved in how species alter
22 their ecosystem and shape its dynamics and functioning. Some theories, such as the metabolic
23 theory of ecology, ecological stoichiometry or pace-of-life theory, already recognize this junction,
24 but only do so in an implicitly non-spatial context. Meanwhile, for a decade now, it has been
25 argued that ecosystem properties have to be understood at a larger scale using meta-ecosystem
26 theory because source-sink dynamics, community assembly and ecosystem stability are all
27 modified by spatial structure. Here, we argue that some ecosystem properties can be linked to a
28 single life-history trait, dispersal, i.e. the tendency of organisms to live, compete and reproduce
29 away from their birth place. By articulating recent theoretical and empirical studies linking
30 ecosystem functioning and dynamics to species dispersal, we aim to highlight both the known
31 connections between life-history traits and ecosystem properties and the unknown areas, which
32 deserve further empirical and theoretical developments.

33 34 **Key words:**

35 community assembly; ecological stoichiometry; ecosystem functioning; metacommunity; meta-
36 ecosystem; metaecosystem; productivity; source-sink dynamics; stability; synchrony

40 The study of life-history traits, *i.e.* traits which influence part of the life cycle of organisms, has
41 historically emerged within population biology with three main objectives: (i) understanding
42 species adaptations to their environments through the evolution of their life cycle (initially
43 dubbed as the study of life-history strategies, e.g. Dingle 1974, Law 1979, Strathmann 1985); (ii)
44 making sense of systematic, apparently non-adaptive phenomena such as senescence in long-
45 lived vertebrates or plants (Hamilton 1966, Reznick et al. 2006, Baudisch et al. 2013, Lemaître et al.
46 2015); and (iii) connecting changes in organism life cycle with their population dynamics through
47 models of age- and stage-structured population demographics (Charlesworth 1994, Caswell 2001).
48 In other words, the initial perspective on life-history traits was driven mainly by evolutionary
49 ecology and population demographics. That is, how life-history traits affect the organism.

50
51 The flip side of the issue is that life-history traits can also be related to the effect of organisms on
52 their environment. Thanks in part to the development of ecological theories linking organism
53 physiology to biogeochemical cycles, most notably ecological stoichiometry (Sterner and Elser
54 2002) and the metabolic theory of ecology (Brown et al. 2004), this initial perspective has recently
55 shifted to incorporate ecosystem functioning and ecological network complexity (e.g. Daufresne
56 and Loreau 2001, Berlow et al. 2009; Box 1 provides a glossary of concepts and technical terms
57 used in this paper). For example, Enquist et al. (1999) proposed linking plant age at reproductive
58 maturity with biomass productivity through allometric relationships between biomass growth,
59 standing biomass and tissue/wood density. According to this theory, wood mass at plant maturity
60 should vary as the fourth power of plant lifespan, thus allowing a rule-of-thumb to calculate the
61 effect of additional extrinsic plant mortality on biomass production. Although empirical evidence
62 behind theories based on allometric relationships is hard to obtain (Nee et al. 2005), it
63 nonetheless relates life-history traits (here, age at maturity) with ecosystem functioning (here,
64 plant productivity and carbon sequestration).

65
66 While ecological stoichiometry and the metabolic theory of ecology have revealed a number of
67 ways that life-history can shape ecosystems (e.g. Elser et al. 2000, Berlow et al. 2009, Hall et al.
68 2011, Ott et al. 2014), these hypotheses lack a proper incorporation of ecological interactions
69 (predation, competition, pollination, parasitism, etc.) and do not take the spatial structure of
70 ecosystems into account. Other work, most notably on host-parasite interactions and the link
71 between life-history strategies and organism immunity, have succeeded in linking life-history
72 traits to parasitic interactions and ecosystem functioning through “pace-of-life” syndromes
73 (Barrett et al. 2008, Réale et al. 2010, Wolf and Weissing 2012, Flick et al. 2016). While pace-of-life
74 theory-based studies do take ecological interactions into account to explain links between life-
75 history traits and ecosystem functioning, they still overlook the spatial structure of ecosystems.

76
77 More recently, metacommunity and meta-ecosystem theories have improved the general
78 understanding of the links between the spatial structure of ecosystems and some of their
79 properties (Loreau et al. 2003b, Leibold et al. 2004, Massol et al. 2011). These include species
80 diversity (Mouquet and Loreau 2003, Gravel et al. 2010b), productivity (Mouquet et al. 2002b,
81 Loreau et al. 2003a), food web interactions (Amarasekare 2008), interaction network complexity
82 (Calcagno et al. 2011, Pillai et al. 2011) and stability (Gounand et al. 2014, Gravel et al. 2016).
83 Nevertheless, though such theories are based on the effects of traits on the dynamics of
84 communities, an explicit link between the metacommunity literature *sensu lato* and life-history
85 theories is still lacking.

86
87 Combining metacommunity ecology with life-history trait ecology has an obvious “trait of
88 choice”: dispersal *i.e.* the tendency of organisms to live, compete and reproduce away from their
89 birth place. The aim of this article is to make explicit the links that connect dispersal, as a life-
90 history trait in the population biology meaning of the word (Bonte and Dahirel this issue), to
91 meta-ecosystem properties using results obtained in the field of metacommunity/meta-

92 ecosystem research. By doing so, we hope to fulfil two objectives: (i) showing how meta-
93 ecosystem theory together with other theories presented above can bridge the gap between life-
94 history trait studies and ecosystem properties; and (ii) identifying remaining questions that still
95 need to be tackled in meta-ecosystem ecology to answer life-history driven questions. We identify
96 theoretical predictions that need experimental testing, as well as needed theoretical
97 developments, to achieve an overall and coherent understanding of natural ecosystems. Below,
98 we first go through effects of dispersal on the functioning of meta-ecosystems. We then describe
99 the effects of dispersal on the dynamics of ecosystems and provide an empirical overview on the
100 life-history traits driving spatial flows between ecosystems and meta-ecosystem properties.
101 Finally, we conclude by discussing interactions between dispersal and other life-history traits in
102 the context of meta-ecosystem ecology, and provide perspectives for future work, both
103 theoretical and empirical.

104 **DISPERSAL AND THE FUNCTIONING OF META-ECOSYSTEMS**

105 Ecosystem functioning is a broad class of properties that involve fluxes and stocks of elements,
106 energy, nutrients or biomass among ecosystem compartments. While traditional, non-spatial
107 ecosystem ecology considers fluxes as the result of primary production (from abiotic
108 compartments to a biotic one), biotic interactions between species (from a biotic compartment
109 to another one), or death and recycling of organic material (from a biotic compartment to an
110 abiotic one), meta-ecosystem ecology acknowledges the existence of a fourth kind of flux, i.e.
111 fluxes due to the physical movement of biotic or abiotic material from one place to another
112 (Massol and Petit 2013). Because dispersal links the functioning of different localities, differences
113 in dispersal can also change the functioning of the entire meta-ecosystem by increasing or
114 decreasing total primary productivity, changing source-sink dynamics among biotic
115 compartments or shift the distribution of biomass across food webs (Loreau and Holt 2004).

116
117
118 Initially studied as a natural extension of the insurance/complementarity hypothesis behind the
119 diversity-productivity relationship (Yachi and Loreau 1999, Norberg et al. 2001), the link between
120 species dispersal and ecosystem productivity was first made explicit for a single trophic level
121 community in the model by Loreau et al. (2003a). The principle behind this model is quite simple:
122 when local environments within patches fluctuate in time (but out-of-phase), dispersal allows
123 species to average their growth rate over several patches and, hence, to perform better than if
124 they had not dispersed. As explained in models of the evolution of dispersal in variable
125 environments, dispersal allows fitness to depend on its arithmetic spatial average rather than
126 geometric temporal average (Metz et al. 1983, Massol and Débarre 2015). This better
127 performance is immediately translated as higher productivity when the species considered in such
128 models are only primary producers (positive green arrow linking “insurance” to “primary
129 productivity” through “temporal variability” on the right-hand side of Fig. 1).

130
131 By contrast, when the environment is spatially heterogeneous, but temporally constant,
132 productivity decreases with dispersal (Mouquet and Loreau 2003), as dispersal maintains
133 maladapted species through source-sink dynamics (Leibold et al. 2004; negative green arrow
134 linking "local adaptation" to "primary productivity" through "quantitative spatial heterogeneity"
135 on the right-hand side of Fig. 1). These results are linked to the effects of dispersal on species
136 coexistence: in the absence of dispersal, local diversity is limited. At very high dispersal, only the
137 best species at the regional level prevails. As a consequence, local diversity peaks at intermediate
138 dispersal, while regional diversity decreases with dispersal (Mouquet and Loreau 2003). Both in
139 the absence or presence of temporal fluctuations of the environment, models based on the
140 insurance hypothesis found positive diversity-productivity relationships in metacommunities
141 (Loreau et al. 2003a, Mouquet and Loreau 2003, Cloern 2007).

143 Primary producer coexistence, and hence productivity following the insurance/complementarity
144 hypothesis, might be improved through spatial structure, i.e. the fact that ecosystems are distinct
145 but connected by dispersal, when producers are constrained by more than one limiting resource
146 (ecological stoichiometry models; see Box 1 and Fig. 2). In the models of Mouquet et al. (2006)
147 and Marleau et al. (2015), nutrient co-limitation, i.e. the “perfect case” for coexistence in the
148 resource-ratio theory (Tilman 1982, 1988), can be obtained through spatial structure and dispersal
149 only. In such a case, resource co-limitation does not exist locally, but emerges at a larger scale due
150 to differences in dispersal rates among functional compartments (Fig. 2B). This emergent effect
151 provides at the same time an explanation for increasing primary producer growth with increasing
152 nutrient concentrations in spite of potential top-down control.

153
154 It is important to consider dispersal as a life-history trait that can have different rates among
155 species within the ecosystem. This can affect ecosystem functioning in the same way that
156 heterogeneity in dispersal rates has been acknowledged, namely as a force shaping species
157 coexistence and diversity distribution within ecological communities (Amarasekare 2003,
158 Calcagno et al. 2006, Laroche et al. 2016). For instance, Gravel et al. (2010a), found that
159 detritus/detritivore or herbivore dispersal, but not that of the basal resource, can enhance
160 primary productivity. Gravel et al. (2010a) also demonstrate that the expected source-sink
161 dynamics of one compartment (e.g. plants) can be reversed when other compartments (e.g.
162 detritus or nutrients) disperse between patches. In particular, the source-sink dynamics of
163 primary producers are sensitive to the balance of nutrient vs. detritus diffusion; patches that
164 would normally be unsuitable for them can become suitable when detritus diffusion rate is high
165 enough (Gravel et al. 2010a; positive green arrow linking detritus to productivity on the left-hand
166 side of Fig. 1).

167
168 A positive or hump-shaped relationship between dispersal and productivity can emerge due to
169 the dual nature of dispersal (i.e. as a flux of material and energy and as a demographic rate,
170 Massol et al. 2011, see Fig. 1). Because dispersal allows the mixing of species across space, it tends
171 to homogenize composition among patches, and thus can have either a positive or a negative
172 effect on productivity depending on whether environmental variability is spatial and/or temporal
173 (Loreau et al. 2003a, Mouquet and Loreau 2003, see the link between “local
174 adaptation”/“insurance” and “characteristics of limiting factors” in Fig. 1). By contrast, any
175 dispersal flux of living organism eventually fuels the detritus pool in the recipient patch and,
176 hence, fertilizes it (left-hand side arrows linking all compartments, except basal resource, to
177 spatial heterogeneity of limiting factors on Fig. 1). Such an enrichment will increase regional
178 productivity because (i) the recipient patch becomes suitable for primary producer if it was not in
179 the first place, and (ii) these fluxes make resource use more efficient overall by preventing
180 nutrient diffusion out of the meta-ecosystem (Gravel et al. 2010a, Fig. 1).

181
182 Other forms of interspecific differences may be important in mediating spatial effects on
183 ecosystem functioning. For instance, Mouquet et al. (2013) proposed the concept of “keystone”
184 and “burden” ecosystems, i.e. local ecosystems that have disproportionately strong positive (for
185 keystone) or negative (for burden) impact on regional productivity. Such effects arise with spatial
186 heterogeneity of the environment and of nutrient inputs. Keystone ecosystems are characterized
187 by relatively high nutrient inputs and dominant primary producers that have the lowest limiting
188 resource requirements. Because ecological stoichiometry is likely linked to demographic
189 parameters (Klausmeier et al. 2004), which in turn have been empirically proved to be connected
190 to life-history traits (Munoz et al. 2016), the road is not long to link interspecific variation in life-
191 history traits to the “keystoneness” of ecosystems in the framework of Mouquet et al. (2013).

192

DISPERSAL AND THE DYNAMICS OF META-ECOSYSTEMS

Ecosystem dynamics refers to the temporal changes of ecosystem variables (e.g. biomass of different compartments) and associated ecosystem properties (e.g. primary productivity). At least three different temporal scales can be distinguished: (i) on long time scales, a dynamical aspect of ecosystems is their assembly, i.e. the building-up of ecosystems by immigration, extinction and evolution of its component species (Morton and Law 1997); (ii) on relatively shorter time scales, the synchrony of different ecosystems connected by dispersal qualifies the coherence of different ecosystem dynamics (Koelle and Vandermeer 2005); (iii) finally, on even shorter time scales, ecosystem stability, in the sense employed by May (1972), is the tendency of systems to return to their initial state after a small perturbation. These three aspects of ecosystem dynamics are linked in complex ways (Briggs and Hoopes 2004), and, as we develop below, are sensitive to the amount of dispersal among ecosystems.

Colonisation and extinction processes are at the heart of the simplest models of ecosystem assembly. The theory of island biogeography (MacArthur and Wilson 1963) has been extended to food webs (Arii and Parrott 2004, Gravel et al. 2011, Cazelles et al. 2015, Massol et al. in press) and has revealed rich and testable predictions (i.e. how many species, trophic levels, etc. can be found on islands relatively to the mainland). These predictions arise from the interplay of two simple rules: predators colonize islands that contain at least one of their prey; and the extinction of a predator's last prey species entails its own extinction on an island. These rules result in island community assembly resembling a sampling of the mainland food web which depends on its topology (Arii and Parrott 2004). In the same way, the strength of extinction cascades triggered by a single random extinction also depend on mainland food web topology (Massol et al. in press).

In food chains, a patch-based metacommunity model predicts that transient food chain assembly within patches submitted to random perturbations depends on top-down effects of predators on prey colonisation and extinction rates (Calcagno et al. 2011). Longer food chains are more likely when predator presence decreases extinction rate and increases colonisation rate (Calcagno et al. 2011). From an evolutionary perspective, an increase of prey extinction rate due to predator occurrence increases the evolutionarily stable dispersal rate in the predator, but is unimodally linked to the evolutionarily stable dispersal rate in the prey (Pillai et al. 2012). Overall, these results suggest that food web assembly – and more generally ecosystem assembly – depends on species dispersal rates in a complex fashion, as predator-induced prey extinction tends to select for more mobility in predator than in prey. When predator presence increases prey extinction rate, foraging by the predator can have the surprising effect of both increasing maximal food chain length while decreasing the average food chain length at the metacommunity scale (Calcagno et al. 2011).

One key finding is that dispersal can substantially modify theoretical predictions of ecosystem stability. May (1972) showed with a simple model of random community matrices that complex and diverse local ecosystems are bound to be unstable. In contrast to May' conclusion, dispersal can substantially increase the stability of diverse and complex ecosystems (Gravel et al. 2016). The general principle is that dispersal tends to stabilize meta-ecosystem dynamics because it averages responses to perturbation. As a result, it buffers extremely strong interaction strengths, which are the most destabilizing. The more ecosystems are “spatially averaged” through dispersal (i.e. the more patches are connected), the more stable the meta-ecosystem can be. Numerical integration of Lotka-Volterra systems (Mougi and Kondoh 2016) and individual-based simulations (Coyte et al. 2015) lead to the same result, with the additional effect that very high dispersal tends to synchronize patch dynamics and thus to “homogenize” ecosystem responses to perturbations,

243 which in turn cancels the stabilizing effect of dispersal (Gravel et al. 2016). Hence, intermediate
244 dispersal rates provide the best conditions for species-rich meta-ecosystem stability.

245
246 The effect of dispersal on the dynamics of simple food web modules in two-patch systems,
247 however, provides contrasting results. Predator dispersal tends to synchronize and destabilize
248 dynamics in both predator-prey (Jansen 2001) and tri-trophic food chains (Jansen 1995). By
249 contrast, in nutrient-detritus-primary producer-consumer systems, nutrient and detritus diffusion
250 rates are destabilizing while producer and consumer dispersal tends to be stabilizing (Gounand et
251 al. 2014). In the latter study, intermediate consumer dispersal rate can lead to alternative stable
252 states of the meta-ecosystem, with the meta-ecosystem being either in a symmetrically oscillating
253 (same dynamics in the two patches) or in an asymmetrically stable state (one patch becomes a
254 source of producers, consumers and detritus while the other stores nutrients) without any
255 underlying heterogeneity of the environment (Gounand et al. 2014).

256

257 **EMPIRICAL FEEDBACK TO THEORY**

258 Empirical work in ecology has been spurred by the theoretical development of the
259 metapopulation and metacommunity concepts, which eventually led to a better understanding of
260 natural ecosystems (e.g. Logue et al. 2011, Grainger and Gilbert 2016). We are now at the point
261 where theoretical developments of the meta-ecosystem concept are also feeding into
262 experimental and comparative studies (e.g. Staddon et al. 2010, Harvey et al. 2016). However,
263 theory on meta-ecosystems is substantially more advanced than its empirical counterpart,
264 possibly because of some inconsistencies between the general models and the specificities of
265 natural systems (Logue et al. 2011). One such inconsistency is the functional nature of the element
266 moving between patches, *i.e.* organisms dispersing vs. material flows. Another potential
267 inconsistency comes from the type of systems that are connected, because theory focuses on
268 fluxes among habitats of the same type, while empiricists have addressed fluxes among different
269 habitat types (habitat is used in this section synonymously to the term biotope). We here
270 exemplify how the meta-ecosystem concept is applied to empirical studies, and discuss this in the
271 context of life-history traits. Based on a text-book example of possible meta-ecosystem dynamics,
272 we identify possible disparities between the theoretical work and its empirical counterparts, and
273 give an outlook on how to resolve the disparities and move forward.

274

275 The main focus of the metacommunity framework is the effect of dispersal on species
276 coexistence, and the most important life-history context is with respect to decisions to disperse
277 or not. Thus, a few dispersing individuals can often have major consequences on the connected
278 communities. Implicitly, even in presence of intense habitat selection, it is assumed that habitats
279 are of similar kind, e.g. different ponds connected by dispersal (Altermatt and Ebert 2010,
280 Declerck et al. 2011). This has been paralleled by extensive experimental work on
281 metacommunities, in which same-type habitats were connected by dispersal (e.g. Cadotte et al.
282 2006, Cadotte 2007, Altermatt et al. 2011, Logue et al. 2011, Grainger and Gilbert 2016). A key
283 finding has been that the species traits related to life history, such as dispersal mode or dispersal
284 stage induction, and life-history trade-offs can strongly affect metacommunity dynamics and
285 species distribution (Altermatt and Ebert 2010, De Bie et al. 2012, Seymour et al. 2015). These
286 studies, for example, found that induction of dispersal stages is linked to environmental
287 deterioration inducing specific life-history stages (dispersal stages), and eventually affecting
288 species' spatial distribution (Altermatt and Ebert 2010, De Bie et al. 2012). Trade-offs between
289 competitive ability and dispersal ability result in distributions of species differing from neutral
290 models assuming otherwise identical life-history traits (Seymour et al. 2015).

291

292 The meta-ecosystem framework explicitly considers local nutrient dynamics and material flows
293 such that dispersing organisms can also be seen as vectors of resources flowing across units of

294 spatial organisation. The theoretical work on meta-ecosystems is indifferent with respect to the
295 identity of these habitat types. Empirically, however, there are two major and distinct scenarios:
296 First, the patches may be of the same habitat type, which would then be an extension of the
297 metacommunity but in which resource flows are also added, e.g. exchange of dispersers and
298 resources among different ponds in a wetland (Howeth and Leibold 2010), intertidal communities
299 (Menge et al. 2015), or litter windblown across different agroecosystems (Shen et al. 2011). The
300 second scenario, and possibly the most common one, however, is that the flows are between
301 different habitat types, such as resource flows between pelagic and benthic habitats, and – more
302 strikingly – between terrestrial and aquatic ecosystems. Massive spatial flows can occur between
303 contrasting ecosystems (Polis et al. 1997) and they are often linked to species life-history,
304 whereby species either transport resources during foraging (e.g. seabirds on islands, Polis and
305 Hurd 1995) or migration, such as excretion of foraging fishes (Bray et al. 1981, Schindler and
306 Scheuerell 2002, Vanni 2002) or feces of large herbivores or migratory birds (Bazely and Jefferies
307 1985, Seagle 2003, Jefferies et al. 2004), or cadavers that serve as resources in the recipient
308 ecosystem without having a population dynamics (e.g. migrating aquatic species in streams,
309 Helfield and Naiman 2002, Naiman et al. 2002, Muehlbauer et al. 2014). Dispersal in the strict sense
310 (Massol et al. 2011) may actually be not feasible between different habitat types for most
311 organisms, as they can only live in one of these habitats and die in the other one. In such a
312 situation, material flows would be the predominant exchange. Thus, in many empirical systems,
313 these material flows are causally linked to the death of organisms (Nakano and Murakami 2001,
314 Sitters et al. 2015), and thus directly depend on life span as one of the most important life-history
315 aspects.

316
317 Most of the empirical examples of strong meta-ecosystem dynamics involve aquatic-terrestrial
318 linkages, in which spatial flows relax each other ecosystem's limitations, e.g. terrestrial carbon
319 input into carbon-limited aquatic systems and converse subsidy of the terrestrial system with
320 aquatic nitrogen (Sitters et al. 2015). A textbook example thereof would be emerging aquatic
321 insects, which can be accidentally diverted into terrestrial systems during their metamorphosis to
322 adulthood and reproductive flights, and subsequently die. Importantly, these organisms, even if
323 moving and mating in the recipient ecosystem, oviposit in the donor ecosystem (aquatic habitat)
324 and do not always actively participate in consumer-resource dynamics in the recipient ecosystem
325 (terrestrial habitat) contrary to what meta-ecosystem models assume regarding organism flows.
326 Flows of aquatic organisms serving as resources in terrestrial systems have been extensively
327 described for aquatic insects but also fish dying after spawning (e.g. Naiman et al. 2002,
328 Muehlbauer et al. 2014, Sitters et al. 2015). However, these studies on strong spatial couplings
329 between ecosystems are mostly found in the ecosystem ecology field literature, with
330 observational data either predating or only marginally linked to the theoretical concept of meta-
331 ecosystems, which historically emerged from the field of population and community ecology
332 (Loreau et al. 2003b).

333
334 In contrast, experimental work on meta-ecosystems has been developed from classic
335 experimental approaches used for metacommunities (Logue et al. 2011, Grainger and Gilbert 2016,
336 Smeti et al. 2016). Such meta-ecosystem experiments have been done almost exclusively using
337 patches of the same type of ecosystem (but see Venail et al. 2008 for an example of microbial
338 communities replicated on different carbon sources), including both dispersal and mass-flows of
339 resources (e.g. Howeth and Leibold 2010, Staddon et al. 2010, Legrand et al. 2012, Livingston et al.
340 2012). These experiments confirm theoretical predictions that meta-ecosystem dynamics can
341 emerge from feedbacks between organism dispersal and resource dynamics in same habitat-type
342 coupled systems, analogous to meta-ecosystem models (first scenario in Fig. 3), such as lake or
343 island networks, or forest patches in an agricultural matrix. However, the important effects that
344 may arise in the emblematic case studies of couplings between ecosystems of different habitat
345 types (second scenario in Fig. 3) have yet to be adequately modelled or experimentally tested.

346

347 Overall, feedback of empirical observations to meta-ecosystem theory leads to the conclusion
348 that the drivers of meta-ecosystem dynamics may differ depending on the scenario of habitat
349 types involved (Fig. 3). In same-habitat-type meta-ecosystems, the spatial structure could be seen
350 as metacommunity-like, with organism dispersal as the dominant spatial flow type, and meta-
351 ecosystem effects would mainly emerge from interactions between dispersal and local resource
352 dynamics (including local recycling). In different-habitat-type meta-ecosystems (e.g. aquatic-
353 terrestrial coupling), the spatial structure mostly consists of material flows (dead organisms with
354 negligible true dispersal), and meta-ecosystem effects would emerge from interactions between
355 material flows and local community dynamics. In the first case, spatial couplings arise from
356 species dispersal traits, while in the second it arises from phenology and life span history-traits.

357

358 We propose that this distinction allows a better identification of the empirical and theoretical
359 work needed: for same-habitat-type meta-ecosystems, we lack observational data to adequately
360 quantify resource flows and we therefore do not yet understand their significance for local
361 dynamics. For different-habitat type meta-ecosystems, flows are well documented, but
362 theoretical models that address the role of organisms which are not dispersing between patches
363 but are instead crossing the barriers to fuel recipient resource pools. In pioneering modelling
364 work, Leroux and Loreau (2012) opened the field by investigating the effects of cross-ecosystem
365 pulsed-flows of herbivores as preys, but further developments in this direction are still needed.
366 On the experimental side, technical challenges have to be addressed to causally separate spatial
367 flows of materials (resources) from spatial flows of organisms (dispersers) (e.g. Harvey et al.
368 2016) in order to be able to test precise meta-ecosystem mechanisms. Empirical questions
369 emerging from this scenario are to test how species life-history traits in one habitat type may
370 cascade to other habitat types through material flows. Furthermore, experimental tests
371 disentangling interactions between perturbation regimes and spatial flows of resources may be
372 highly relevant from an applied empirical perspective, and can be addressed in an explicit meta-
373 ecosystem perspective. Ultimately, we expect the dynamic interplay of theory (e.g. Loreau et al.
374 2003b, Massol et al. 2011, Gounand et al. 2014) and empirical work to lead to a better and more
375 mechanistic understanding of spatial community and ecosystems dynamics.

376

377 **DISCUSSION**

378 **Dispersal: a life-history trait with many effects on ecosystems**

379 Previous sections have emphasized some ecosystem properties that are affected by dispersal
380 within meta-ecosystems. First, depending on species coexistence mechanisms, dispersal tends to
381 increase local diversity and to increase meta-ecosystem productivity, at least until intermediate
382 levels of dispersal (Levin 1974, Mouquet and Loreau 2002, Loreau et al. 2003a, Economo and Keitt
383 2008). Second, provided patches are sufficiently heterogeneous in their response to
384 perturbations, dispersal stabilizes meta-ecosystem dynamics (Gravel et al. 2016, Mougi and
385 Kondoh 2016), although the dispersal of some trophic levels is more stabilizing than others
386 (Gounand et al. 2014). Third, in simple interaction networks, dispersal tends to synchronize and
387 destabilize local dynamics (Jansen 1995, 2001) while limited dispersal increases persistence of
388 otherwise ephemeral species assemblages (Briggs and Hoopes 2004). Fourth, in spatially
389 structured heterogeneous ecosystems, dispersal paves the way for nutrient co-limitation and
390 hence for species coexistence on a few limiting resources (Mouquet et al. 2006, Marleau et al.
391 2015). On top of these effects of dispersal on ecosystem functioning and dynamics, species
392 dispersal/colonization abilities shape food web complexity (Calcagno et al. 2011, Pillai et al. 2011),
393 which can potentially feedback on ecosystem stability (Allesina and Tang 2012, Neutel and Thorne
394 2014, Grilli et al. 2016).

395

396 Meta-ecosystem theory is not solely geared towards understanding the functioning of
397 ecosystems, but also grounded in the foundations laid out by metapopulation and
398 metacommunity theories. Therefore, the movements of species within a meta-ecosystem are
399 bound to be governed by how organisms perceive their environment and where they thrive – i.e.
400 non-random dispersal, habitat selection, foraging and dispersal evolution (Amarasekare 2008).
401 The feedback of meta-ecosystem state on dispersal evolution has just begun to be studied, and
402 has focused so far on simple predator-prey configurations (Chaianunporn and Hovestadt 2012,
403 Pillai et al. 2012, Drown et al. 2013, Travis et al. 2013, Amarasekare 2015). On top of all the
404 mechanisms of dispersal evolution that are already known (Bowler and Benton 2005, Ronce 2007,
405 Duputié and Massol 2013), meta-ecosystem context is likely to provide new selection mechanisms
406 through the discrepancy in generation time and spatial scale of motility of different trophic levels.
407 For instance, dispersal is selected against when environmental quality of habitat patches is
408 positively autocorrelated in time, but selected for when it is positively autocorrelated in space
409 (Travis 2001, Massol and Débarre 2015). In the case of a prey species for which predator presence
410 is an “environmental characteristic”, as predators live longer, have slower population dynamics
411 and can cover and forage over several prey patches at once, the “effective” autocorrelation of
412 the environment for the prey will likely be positive in both time and space, thus affecting the
413 evolution of prey dispersal. Evolution of dispersal in food webs also imposes a feedback between
414 the cost of dispersal and dispersal itself, as sparse prey populations can diminish predation
415 pressure and, hence, decrease the cost of dispersal borne out of predation between habitat
416 patches. Finally, it is also noteworthy that, even though dispersal evolution has begun being
417 considered in a food web context, the consequences of this evolution on ecosystem functioning
418 have yet to be studied.

419

420 **Other life-history traits and their impact on meta-ecosystems**

421 The central tenet of meta-ecosystem studies is that species dispersal may be responsible for many
422 patterns that would otherwise require more complicated theories to explain, such as the
423 maintenance of maladapted species (the “mass effect” paradigm of metacommunity theory,
424 Shmida and Wilson 1985, Leibold et al. 2004) or the distribution of species abundance in
425 ecological samples, as predicted by the neutral theory of ecology (Hubbell 2001, Volkov et al.
426 2003). From this central tenet, it is no wonder that the main connection made by these studies
427 between life-history traits and ecosystem properties considers dispersal as the life-history trait of
428 interest. However, dispersal generally correlates with a wide palette of other traits (e.g.
429 fecundity, body size, etc., see Bonte and Doherty this issue), known collectively as “dispersal
430 syndromes” (Clobert et al. 2009, Ronce and Clobert 2012, Duputié and Massol 2013). Such
431 correlations can be explained in three ways: (i) the other trait correlates with dispersal ability
432 because there is a trade-off constraining the values of both traits (e.g. time allocation trade-off
433 preventing an organism from both moving and eating at the same time); (ii) dispersal correlates
434 with the other trait because both traits are structurally linked, e.g. they both scale with organism
435 size (allometric link) or they both respond similarly to biological stoichiometric changes
436 (stoichiometric link); (iii) both dispersal and the other trait are shaped by joint selective pressures,
437 with either the same pressures acting on both traits at once (e.g. dormancy and dispersal, Vitalis
438 et al. 2013) or one or both trait(s) having a selective feedback on the other (e.g. selfing and
439 dispersal, Cheptou and Massol 2009, or local adaptation and dispersal, Berdahl et al. 2015). In
440 practice, correlations between dispersal and other life-history traits can only be uncovered when
441 there is sufficient variation in the traits under study, which means that the wider “the
442 phylogenetic net”, the easier it is to capture such correlations. However, interpreting these
443 correlations as resulting from trade-offs, structural constraints or joint evolution is often difficult
444 and experimentally challenging, especially when the problem is framed as the inference of life-
445 history invariants (Nee et al. 2005).

446

447 It would be difficult to enumerate here all the possibilities of dispersal-trait correlations that
448 would likely have impacts on meta-ecosystem functioning and dynamics. Some of these have
449 already been considered separately. For example, Otto et al. (2007)'s study on the effect of
450 predator-prey body mass ratios on food web stability could be easily coupled with Gravel et al.
451 (2016)'s study on the effect of dispersal on ecosystem stability to gain insight into the combined
452 effects of dispersal and body size when both traits are structurally linked. Others readily lend
453 themselves to speculation. For example, with higher passive dispersal in smaller organisms and
454 the relationship between initial growth, asymptotic size and temperature in ectotherms (Atkinson
455 et al. 2006), one is tempted to think that warming oceans might become less connected by
456 dispersal, as some data on larval dispersal already suggest (O'Connor et al. 2007), which in turn
457 would affect their functioning and dynamics as predicted by the models described in previous
458 sections.

459 An especially challenging issue regarding life-history trait evolution and meta-ecosystem
460 properties is to link ecological stoichiometry with ecosystem properties through cell and
461 organism physiology (Jeyasingh and Weider 2007), e.g. as proteins and rRNA have different
462 stoichiometry (Loladze and Elser 2011). For instance, the proportion of phosphorus content due to
463 RNA (vs. due to skeleton) is expected to decrease with body mass in vertebrates (Gillooly et al.
464 2005). In some insects, high-dispersal genotypes are associated with particular alleles at genes
465 coding for phosphoglucose isomerase (PGI), e.g. in the Glanville fritillary butterfly (Haag et al.
466 2005, Hanski and Saccheri 2006). Efficient PGI genotypes have a higher peak metabolic rate and
467 fly longer than less efficient types (Niitepõld et al. 2009, Niitepõld and Hanski 2013). As the PGI
468 enzyme is involved in glycolysis and gluconeogenesis, a link between PGI and ecological
469 stoichiometry might be expected (as suggested by experimental evidence on *Daphnia pulex*,
470 Jeyasingh and Weider 2005, Weider et al. 2005) which, in turn, would link ecological stoichiometry
471 with dispersal ability. This field of inquiry is just beginning, but might reveal exceptional findings
472 linking traits and ecosystem functioning, such as an increased spatial diffusion of one type of
473 nutrient over another one due to a systematic association of body stoichiometry with dispersal
474 rate.
475

476 **Challenges ahead for meta-ecosystem ecology**

477 The study – both theoretical and empirical – of mechanisms linking organism dispersal and
478 ecosystem properties is a recent endeavour in ecology. To date, meta-ecosystem ecology has
479 focused on linking community ecology (species coexistence, distribution of diversity), with
480 ecological dynamics and demographics (ecosystem stability, synchrony, assembly), ecological
481 interaction networks (network complexity, material/energy fluxes) and functional ecology
482 (stocks, fluxes and productivity). However, two interfaces have yet to be strengthened with
483 respect to life-history traits and meta-ecosystem properties.
484

485 First, the integration of biogeography and functional ecology through meta-ecosystems has only
486 begun to be addressed (Wieters et al. 2008, Meynard et al. 2011, Kissling et al. 2012, Nogales et al.
487 2015). This interface between meta-ecosystem ecology and biogeography is a necessary step if we
488 are to extend species distribution models and other map-based representations of biodiversity to
489 map-based representations of ecosystem functioning and linking these with the underlying
490 mechanisms involved. As life-history traits play key roles in determining species response to
491 anthropically driven changes of the environment (Lindborg 2007, Colautti et al. 2010, Ojanen et al.
492 2013), life-history traits, and dispersal in particular, will probably play a key role in explaining
493 spatial distribution of ecosystem functioning.
494

495 Second, we can ask whether variability in life-history traits such as dispersal may entail direct
496 consequences for ecosystem properties. For instance, Laroche et al. (2016) recently studied the
497

498 evolution of dispersal in a model based on Hubbell's (2001) neutral model of biodiversity to assess
499 whether species would converge or diverge in dispersal rate. As it turned out, diversity patterns
500 are strongly altered by disruptive selection on dispersal (Laroche et al. 2016). Speculation linking
501 these results with others from meta-ecosystem models (e.g. Gounand et al. 2014) may lead us to
502 think heterogeneous selection on dispersal rates among trophic levels could drive eco-
503 evolutionary feedbacks linking dispersal evolution and ecosystem functioning.

504
505

506 **Closing words: empirical and theoretical directions**

507 We list here several important directions that deserve further enquiry, both on the empirical and
508 theoretical fronts. Meta-ecosystem ecology and its interface with life-history studies in particular
509 need to be strengthened by making experiments to test important meta-ecosystem predictions
510 and by developing meta-ecosystem models in directions that will more strongly link them to life-
511 history traits:

- 512 (i) The maximization of ecosystem productivity at intermediate dispersal has to be tested with
513 respect to the mechanisms maintaining coexistence of primary producers (Mouquet et al.
514 2002a, but see Howeth and Leibold 2008), and the effect of dispersal asymmetries between
515 trophic levels on productivity (Gravel et al. 2010a) needs experimental support.
- 516 (ii) Experimental studies are required to explore whether different ecosystem functions are
517 affected differently by the movements of nutrients, detritus, primary producers, consumers,
518 etc. Existing models suggest that dispersal asymmetries can do more than just alter patch
519 source-sink status (Gounand et al. 2014) and existing experiments point out possible effects
520 of basal species dispersal on species regulation processes (Howeth and Leibold 2008).
- 521 (iii) The general prediction that intermediate dispersal rates should stabilize meta-ecosystems
522 has to be tested properly, both experimentally (but see Howeth and Leibold 2010, 2013), and
523 based on large-scale observational datasets of abundance time series (following the
524 approach of Jacquet et al. 2016).
- 525 (iv) The idea of spatial complementarity between habitats within a meta-ecosystem needs to be
526 assessed and experimentally challenged. For instance, when ecosystems are intrinsically
527 limited by different nutrients in different habitats (e.g. C in aquatic habitats vs. N in terrestrial
528 ones), experiments are needed to assess whether intermediate (or high) spatial flows of
529 biotic compartments lead to higher productivity.
- 530 (v) Experiments should test whether spatial structure and heterogeneity of supply points can
531 lead to the stable coexistence of species with different resource ratios (Mouquet et al. 2006,
532 Marleau et al. 2015), possibly exploring situations more complicated than two-patch, two-
533 species, two-resource systems.
- 534 (vi) Theoretical studies are needed to explore how perturbations propagate within a meta-
535 ecosystem, depending on which compartments are dispersing more, on connectivity
536 patterns, on first-disturbed compartments and on the nature of the perturbation (invasion,
537 extinction, habitat destruction, etc.), following new perspectives on the notion of stability in
538 ecology (Arnoldi et al. 2016).
- 539 (vii) One promising theoretical endeavour would be to predict the impact of ecosystem removals
540 on diversity and functioning in a spatially explicit fashion, thus merging models of Economo
541 and Keitt (2008, 2010) on diversity in metacommunity networks and Mouquet et al. (2013) on
542 keystone ecosystems.
- 543 (viii) Species coevolution models are highly needed to assess whether evolution leads to increases
544 or decreases in productivity, fluxes, synchronicity, stability, etc. at the meta-ecosystem scale,
545 e.g. focusing on the evolution of dispersal at different trophic levels within food webs.
- 546 (ix) Models of ecosystem assembly and disassembly should be developed to assess the conditions
547 of existence of "forks" (i.e. alternative trajectories), "dead-ends" or loops in the topology of
548 ecosystem successions (Law and Morton 1993).

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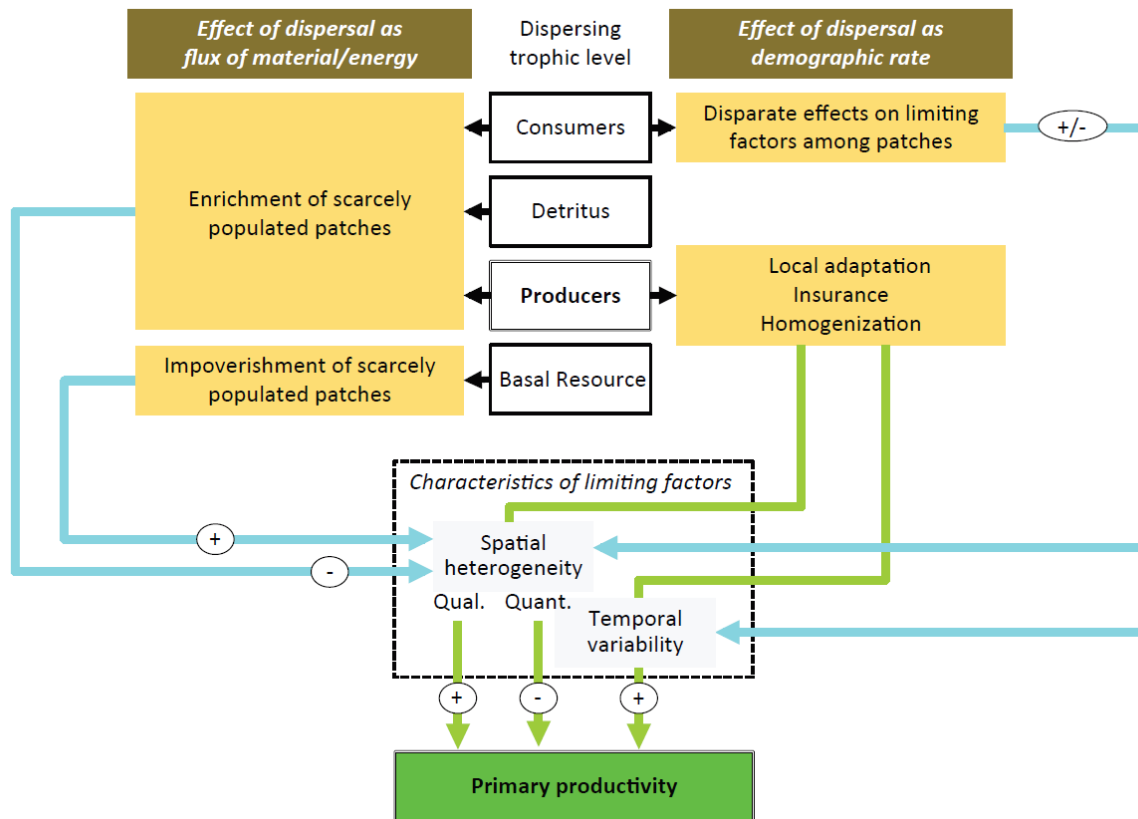
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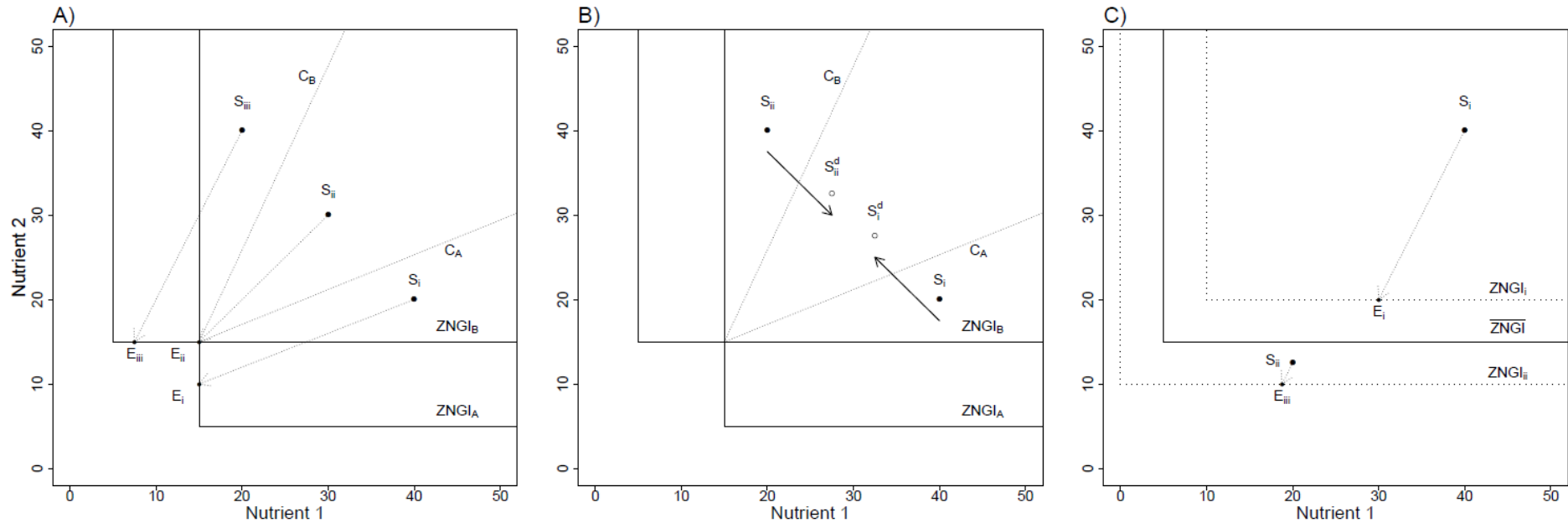
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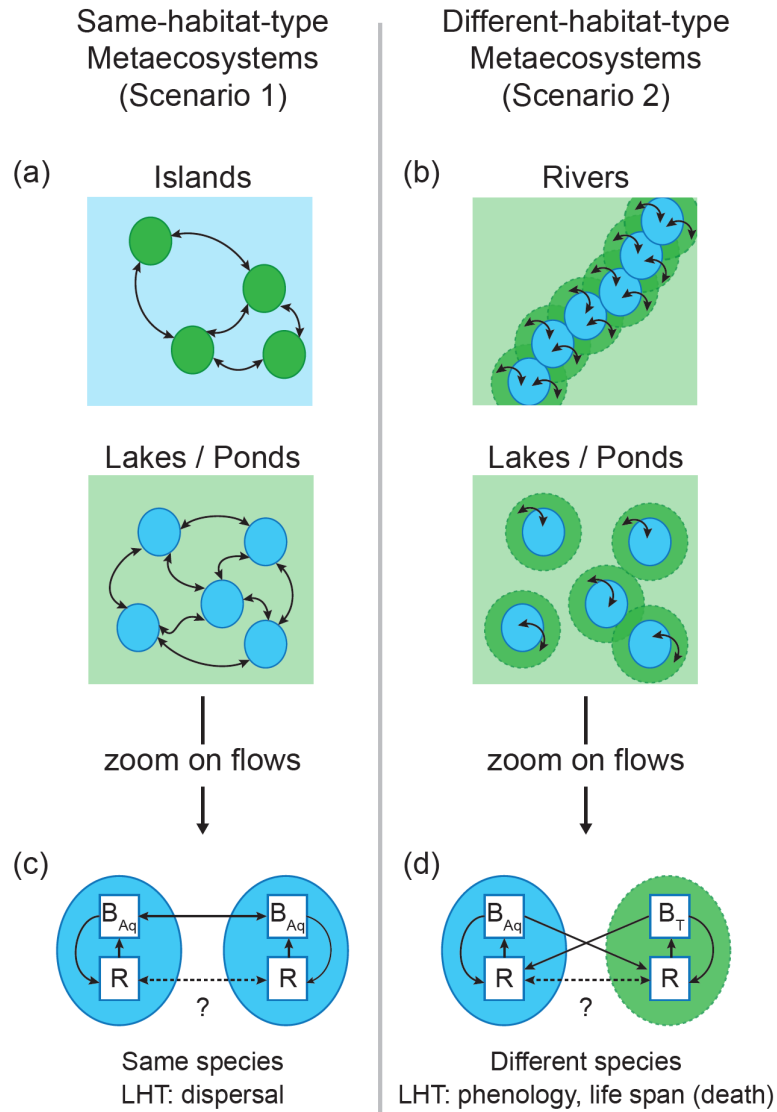


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 938 **Fig. 1** – Links between dispersal and primary productivity according to meta-ecosystem theory
 939 (Loreau et al. 2003a, Mouquet and Loreau 2003, Gravel et al. 2010a). On the left-hand side of the
 940 diagram, dispersal of consumers, detritus and producers, seen as fluxes of material and energy,
 941 tends to increase the amount of biomass in scarcely populated patches (i.e. those in which basal
 942 resource levels are too low for the establishment of producers and/or consumers) and thus,
 943 through nutrient recycling, to decrease the spatial heterogeneity in nutrient stocks among
 944 patches (low blue arrow with a minus sign). Diffusion of the basal resource, nutrients (Gounand
 945 et al. 2014), or producers seen as basal resource (Pedersen et al. 2016), on the other hand,
 946 will create a source-sink movement from low-productivity patches to already highly productive
 947 patches, thus aggravating the spatial heterogeneity of resource stocks among patches (long blue
 948 arrow with a plus sign). Spatially heterogeneous distribution of a single resource results in a
 949 negative effect on primary productivity (quantitative heterogeneity). However, in case of several
 950 resources, heterogeneity in local nutrient balances (qualitative heterogeneity) may lead to
 951 positive effects on productivity (Marleau et al. 2015). On the right-hand side of the diagram,
 952 dispersal of primary producers seen as a demographic rate (i.e. the I and E of the BIDE framework
 953 proposed by Pulliam 1988) generally decreases local adaptation of primary producers (they end
 954 up in patches in which they are less well adapted, but see Edelaar and Bolnick 2012 for possible
 955 counter-examples), but primary productivity provided by the community of primary producers
 956 gains “insurance” against temporal variability of the environment. Dispersal thus increases
 957 productivity at the regional scale when the environment is temporally variable, but decreases it
 958 when it is spatially heterogeneous (green arrows going through spatial heterogeneity and spatial
 959 variability of limiting factors); the combination of the two results in a hump-shaped link between
 960 dispersal and productivity. The blue arrows on the right-hand side of the diagram represent the
 961 potential demographic effects of consumer dispersal on limiting factor variability in time and
 962 space; as this effect is quite variable across scenarios, its effect on productivity is far from being
 963 predictable (Jansen 1995, 2001, Koelle and Vandermeer 2005, Gounand et al. 2014).



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966 **Fig. 2** – Graphical interpretation of the resource-ratio theory in a competitive meta-ecosystem. A) Representation of a single ecosystem made of two
967 resources and two competitors. Stable coexistence will depend on where the supply point S_i is located relative to the projection of the consumption
968 vectors C_A and C_B . Equilibrium nutrient availability is indicated by the E_i and the location depends on the final species composition. B) Conceptual
969 representation of source-sink dynamics of inorganic nutrients in a two-patch meta-ecosystem. The location of the two supply points is moved toward
970 the centre of the nutrient space, to locations S_i^* , resulting in the homogenization of the metacommunity. Regional coexistence is possible in absence
971 of nutrient movement, but not local coexistence. The movement of net supply points toward the centre, however, allows local coexistence of the two
972 species. C) Representation of the effect of dispersal of a single species on the location of the ZNGIs in presence of source-sink dynamics. The ZNGI
973 moves to the bottom left in the patch ii (a sink), because of immigration, allowing its stable persistence there. Similarly, the ZNGI moves to the top
974 right in patch i (a source), consequent to emigration.



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Fig. 3 – Two contrasting meta-ecosystem types based on empirical observations and illustrated by aquatic – terrestrial landscapes. Panels (a) and (b) give examples of spatially structured landscapes in which habitat patches are connected by spatial flows (arrows). Blue and green colours refer to aquatic and terrestrial respectively. Left column shows meta-ecosystems in which patches are of same habitat type, while right column shows meta-ecosystems in which patches are of different habitat types. If we zoom on documented flows between two patches (bottom panels), same-habitat-type meta-ecosystems (c) are mostly linked by organism dispersal and potential flows of resource (R), but these are poorly documented (dotted arrows). Different-habitat-type meta-ecosystems (d) are linked by exchanges of dead organisms fuelling the resource pool. B_{Aq} , and B_T refer to biomass of aquatic and terrestrial organisms respectively.

986 **BOX 1: GLOSSARY**

987

988 **Ecological stoichiometry:** The study of element (e.g. carbon, nitrogen, phosphorus...) content
989 within organisms and its stocks and fluxes involved in ecological processes at larger scales.

990

991 **Keystone and burden ecosystems:** An ecosystem is said to be “keystone” if its removal from the
992 meta-ecosystem leads to disproportionately deleterious consequences for a given (or several)
993 ecosystem property (e.g. productivity) at the meta-ecosystem scale. Conversely, a burden
994 ecosystem’s removal leads to disproportionately beneficial consequences at the meta-ecosystem
995 scale. The definition of “disproportionately” in this context is based on what the removal of a
996 typical ecosystem of the same “size” would entail at the meta-ecosystem scale (Mouquet et al.
997 2013).

998

999 **Metabolic theory of ecology:** A theory which links the different rates involved in organism life
1000 history (growth, consumption, death, etc.) with body size and temperature through chemical and
1001 physical processes and laws (Brown et al. 2004).

1002

1003 **Neutral theory of community ecology:** A theory which explains the diversity of species observed
1004 in ecological communities solely through the interplay of stochastic processes (dispersal,
1005 ecological drift, speciation, remote colonization) and not through species niche (Hubbell 2001).

1006

1007 **“Pace-of-life” theory of animal personality syndromes:** A theory which posits that natural
1008 selection generally leads to the existence of general personality syndromes linking physiological,
1009 immunological, foraging and life-history traits (Réale et al. 2010).

1010

1011 **Resource ratio theory:** A theory which explains the coexistence of species based on the
1012 complementarity of their resource needs and their impacts on resource stocks (León and
1013 Tumpson 1975, Tilman 1980, 1982). This theory has been expanded since then to include other
1014 limiting factors, such as predator pressure (Leibold 1995).

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1018 **BOX 2: DISPERSAL AND STOICHIOMETRY IN META-ECOSYSTEMS**

1019 The resource-ratio theory of plant coexistence (Tilman 1982, 1988), based on the seminal model of
1020 León and Tumpson (1975), has been instrumental in our understanding of the intimate linkage
1021 between stoichiometry, community assembly and ecosystem functioning. The theory applies to
1022 two resources the R^* principle of competition theory. Its main prediction is that stable
1023 coexistence between two species requires a particular ratio of the two limiting nutrients. Owing
1024 to its accessible graphical representation, the theory has a central position in most ecological
1025 textbooks (e.g. Begon et al. 2006). The theory was also further developed to derive a vast array
1026 of secondary predictions, such as the impact of resource heterogeneity and fertilization on
1027 species richness and successional dynamics (Tilman 1982, 1985). The resource ratio theory builds
1028 on the idea that spatial heterogeneity in the ratio of limiting resources promotes the maintenance
1029 of highly diverse communities (Tilman 1982). This prediction does apply to various spatial scales,
1030 from the individual-to-individual variation in soil properties, to landscape variations. The theory
1031 does not, however, consider the impact of spatial exchanges of plants, nutrients and other
1032 materials between localities. Both metacommunity (Mouquet and Loreau 2002, Abrams and
1033 Wilson 2004) and meta-ecosystem (Gravel et al. 2010a) theories in source-sinks settings have
1034 shown that the outcome of competitive interactions could be significantly altered by these flows.
1035 While it is quite challenging to elaborate a full and comprehensive theory for stoichiometry of
1036 nutrient flows in source-sink meta-ecosystems, it is nonetheless possible to get some intuition
1037 from a graphical representation of two patches and two nutrients.

1038
1039 The graphical interpretation of the resource-ratio theory builds on a few important concepts.
1040 First, the Zero Net Growth Isocline (ZNGI) represents the combination of the two nutrient
1041 concentrations resulting in a null intrinsic growth rate for a given species (Fig. 2). In other words,
1042 it is the two-dimensional representation of the R^* principle of competition theory. Nutrients are
1043 supplied at a given ratio in any locality, owing to processes such as atmospheric depositions on
1044 land and river and stream inflows in lakes. In absence of consumption by primary producers, the
1045 nutrients do equilibrate to a given concentration and ratio, represented visually as the supply
1046 point S (Fig. 2). A key concept is that a species is able to persist provided that the supply point is
1047 located somewhere above its ZNGI. Once a species establishes, it consumes nutrients in a given
1048 ratio, which is represented by the consumption vector (the slope of the vector corresponds to the
1049 ratio of nutrient consumption). The system will converge at equilibrium to the point
1050 corresponding to the intersection between the ZNGI and the consumption vector aligned on the
1051 supply point. Coexistence of two species occurs provided that their ZNGIs do cross each other,
1052 and that the supply point is located in the triangle defined by the projection of their respective
1053 consumption vectors (Fig. 2; Tilman 1982, 1988). When limiting factors are not resources, but
1054 natural enemies (i.e. the case in models of apparent competition), the same approach can also be
1055 used (Leibold 1995, Grover and Holt 1998), although ZNGIs and the conclusions associated with
1056 the different angles of intersections are not defined in exactly the same way, and nonlinearities in
1057 predator functional responses can lead to departures from resource-ratio theory (Grover and Holt
1058 1998).

1059
1060 Nutrient cycling and any spatial exchange of nutrients between localities, whether inorganic or
1061 sequestered in biomass, significantly complicate the situation and often make the underlying
1062 mathematics intractable. But fortunately, the concept is pretty straightforward to illustrate
1063 graphically. In both cases, they represent an additional source of nutrient inputs and therefore
1064 move the supply point in the two-nutrient space. In the simple case of decomposition of detritus,
1065 where both nutrients are mineralized at the same rate, we do find the net supply point (S')
1066 moving away from its original location. It increases the fertility of the system, but does not
1067 change the equilibrium situation because it keeps the same ratio. The net supply point will,
1068 however, move in one direction or another if the mineralization or the dispersal between

1069 localities does not respect the ratio at which it is consumed. For mineralization to alter the
1070 conditions for coexistence, it requires that the net supply point S' is located within the projection
1071 of the two consumption vectors (Daufresne and Hedin 2005).

1072
1073 The situation is slightly more complicated for nutrient diffusion, in particular when the two
1074 localities do have different nutrient supplies, or alternatively if they are occupied by different
1075 species with distinct ZNGIs and consumption vectors. If the movement of nutrients is passive, it
1076 will move by diffusion from the locality that has the highest nutrient concentration (the source)
1077 to the locality with the lowest nutrient concentration (the sink). The location of the net supply
1078 point will therefore move in both localities. If the two localities are occupied by the same species,
1079 it will inevitably move the supply point toward the centre of the nutrient space, as it will
1080 homogenize the meta-ecosystem. It could, however, go in the other direction depending on the
1081 characteristics of each species inhabiting localities. As a consequence, each nutrient in a patch
1082 could thus either increase or decrease in availability, thus eventually affecting the conditions for
1083 coexistence.

1084
1085 Finally, organisms themselves can move across the patches. The impact of their dispersal has
1086 been extensively studied in a wide range of conditions (e.g. Amarasekare and Nisbet 2001,
1087 Mouquet and Loreau 2002, Abrams and Wilson 2004). Again, often the mathematics is hard to
1088 track in all of these models, but the graphical representation provides a useful and general
1089 understanding of the consequences of source-sink dynamics on species coexistence. Basically,
1090 dispersal inflicts an increased loss of individuals in the location with highest density (emigration
1091 from the source), and an enrichment in the location with lowest density (immigration to the sink).
1092 It provokes a translation of ZNGIs for both nutrients (Fig. 2), moving them to higher values in the
1093 source location and to lower values in the sink. As a consequence, dispersal might sustain a
1094 population in a location that would be otherwise inhospitable, as in traditional source-sink
1095 systems (Pulliam 1988) or in competitive systems (Mouquet and Loreau 2002). The projection of
1096 the consumption vectors will not be altered by dispersal of the organisms, even if there is nutrient
1097 cycling of their detritus, except in the case in which the two nutrients are not recycled at the
1098 same rate.

1099
1100 In conclusion, spatial exchanges of nutrients, organisms and their detritus might alter the
1101 conditions for coexistence. They tend to promote regional coexistence in presence of spatial
1102 heterogeneity of supply points because (i) the supply point moves toward the centre of the
1103 nutrient space, thereby making the conditions for coexistence more likely, and (ii) the ZNGIs
1104 move in a way that increases the tolerance of species to harsh conditions and decreases their
1105 performance in good locations. More extensive analyses also show that it can lead to alternative
1106 stable states, and potentially dynamic instabilities (Daufresne and Hedin 2005; Gravel et al.,
1107 unpublished manuscript). Another consequence is that dispersal, of all kinds, tends to
1108 homogenize the meta-ecosystem in most situations.

1109