

## Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes

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Abstract:	Habitat fragmentation, an important element of current global change, has profound repercussions on population and species extinction. Landscape fragmentation reduces individual movements between patches (i.e. dispersal) while such movements connecting patches enhance the persistence of metapopulations and metacommunities. Through the recognition of non-random movements, dispersal has recently been recognized as a highly complex process. This complexity likely changes the predictions on the evolution of dispersal in spatially structured populations and communities. In this article, we emphasize the effects of fragmentation on the evolution of non-random dispersal. Habitat fragmentation may shape local and global selective pressures acting on a large array of phenotypic traits known to covary with dispersal behaviors. On top of changes in dispersal propensity, habitat fragmentation could therefore modify dispersal syndromes (i.e. dispersers' phenotypic specializations). Habitat fragmentation often leads to spatial structuring of local conditions and consequently may lead to the evolution of different dispersal syndromes at the landscape scale. By neglecting impacts on dispersal syndromes, we might underestimate the impacts of fragmentation on a crucial biodiversity level for metapopulation and metacommunity functioning. We highlight a set of priorities for future empirical and theoretical work that together would provide the understanding of eco-evolutionary dynamics of dispersal syndromes required for improving our ability to predict and manage spatially structured populations and communities.



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1 **Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes**

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26 **Abstract**

27

28 Habitat fragmentation, an important element of current global change, has profound  
29 repercussions on population and species extinction. Landscape fragmentation reduces  
30 individual movements between patches (i.e. dispersal) while such movements connecting  
31 patches enhance the persistence of metapopulations and metacommunities. Through the  
32 recognition of non-random movements, dispersal has recently been recognized as a highly  
33 complex process. This complexity likely changes the predictions on the evolution of dispersal  
34 in spatially structured populations and communities. In this article, we emphasize the effects  
35 of fragmentation on the evolution of non-random dispersal. Habitat fragmentation may shape  
36 local and global selective pressures acting on a large array of phenotypic traits known to  
37 covary with dispersal behaviors. On top of changes in dispersal propensity, habitat  
38 fragmentation could therefore modify dispersal syndromes (i.e. dispersers' phenotypic  
39 specializations). Habitat fragmentation often leads to spatial structuring of local conditions  
40 and consequently may lead to the evolution of different dispersal syndromes at the landscape  
41 scale. By neglecting impacts on dispersal syndromes, we might underestimate the impacts of  
42 fragmentation on a crucial biodiversity level for metapopulation and metacommunity  
43 functioning. We highlight a set of priorities for future empirical and theoretical work that  
44 together would provide the understanding of eco-evolutionary dynamics of dispersal  
45 syndromes required for improving our ability to predict and manage spatially structured  
46 populations and communities.

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**48 Introduction: the multidimensional dispersal process**

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Habitat conversion from natural ecosystems to agriculture, forestry and human settlements has taken over large amounts of land, leaving species with an increasingly shrinking world (Foley et al. 2005, Newbold et al. 2015). Beyond direct negative effects on taxonomic, functional and genetic diversity (Foley et al. 2005, Newbold et al. 2015), this indirectly erodes biodiversity through the fragmentation of large, continuous habitats into smaller isolated patches in a sea of often heterogeneous matrix (Resasco et al. in press, Thompson et al. in press, Fahrig 2003, Haddad et al. 2015, Wilson et al. 2015). Fragmentation modifies landscapes in four ways -- reducing habitat quantity; increasing the number of patches; decreasing their size; and, increasing isolation (Fahrig 2003) -- with diverse effects on population dynamics. Smaller patches have smaller populations, increasing stochastic risks of extinction from demographic and genetic processes, e.g. inbreeding depression, leading to an extinction vortex (e.g. Gilpin 1986, Fagan and Holmes 2006). Moreover, increasing inter-patch distances magnifies dispersal risks; fragmentation may reduce movements among patches (Fahrig 2007) and worsen the extinction vortex. Dispersal between patches (Fahrig and Merriam 1994, Baguette et al. 2013), enables recolonization after local extinction and may even reduce the likelihood of stochastic extinctions (Fahrig and Merriam 1994, Bowne and Bowers 2004, Baguette et al. 2013). The precise influence of dispersal on population persistence depends on both landscape and dispersal traits (Johst et al. 2002, Vuilleumier and Possingham 2006). Increased dispersal may even hamper persistence, given trade-offs with reproduction (Baguette and Schtickzelle 2006), effects on synchrony (Heino et al. 1997), or the swamping of local adaptation (Lenormand 2002). Understanding how dispersal will change post-fragmentation (including via evolution) is essential for forecasting the fate of populations and communities (Caplat et al. 2016).

73           Dispersal is increasingly recognized to be a complex process. A major advance is  
74 recognizing inter-individual variability in dispersal (Clobert et al. 2009). Dispersers are not a  
75 random draw from a population, moving across a landscape at fixed rates. Rather, dispersal  
76 decisions depend on individual phenotypes and environments (i.e. context- and/or phenotype-  
77 dependent dispersal) at each of three dispersal steps: departure (emigration), transience, and  
78 settlement (immigration); e.g. (Holt 1987, Armsworth and Roughgarden 2005a, Bowler and  
79 Benton 2005, Benard and McCauley 2008, Clobert et al. 2009, Delgado et al. 2010, Lowe and  
80 McPeck 2014). Inter-individual variability in dispersal arises from variability in phenotypic  
81 traits (e.g. morphology, physiology, behavior) through: 1) *enabling traits* - phenotypes  
82 required to disperse at all (e.g. presence of wings, ballooning behavior; 2) *enhancing traits* -  
83 phenotypes facilitating dispersal or reducing its costs (e.g. longer wings, higher energy  
84 reserves); 3) *matching traits*, leading to non-random movements, conditional on other  
85 phenotypic traits and dispersal drivers (e.g., local conditions). The phenotype of an individual  
86 may imply higher fitness in specific environments (Levins 1962), which should select for  
87 inter-individual movement differences in a heterogeneous landscape (e.g. Baguette and Van  
88 Dyck 2007, Clobert et al. 2009) and covariances between dispersal decisions and a suite of  
89 phenotypic traits, which we call *dispersal syndromes* (Clobert et al. 2009). Such phenotypic  
90 dependency may arise at any of the three steps of dispersal so that individuals find and settle  
91 in habitats that best match their phenotypes and maximize their fitness (Maynard-Smith 1966,  
92 Holt 1987, Ruxton and Rohani 1999, Ravigné et al. 2004, Armsworth and Roughgarden  
93 2005a, Edelaar et al. 2008). Non-random dispersal (i.e. context- or phenotype-dependent  
94 dispersal) is likely the rule rather than the exception. Species dispersal decisions at any stage  
95 should depend on external factors (abiotic and biotic conditions) or internal factors (genetic,  
96 physiology, morphology and behavior), well beyond habitat matching (i.e. phenotype-  
97 dependent habitat preference, Berner and Thibert-Plante 2015). Despite mounting empirical

108 evidence of non-random dispersal (Edelaar and Bolnick 2012), it is not yet often incorporated  
109 into empirical and theoretical studies of spatially structured population and community  
100 dynamics (but see e.g. Fogarty et al. 2011, Bolnick and Otto 2013, Bocedi et al. 2014, Henry  
101 et al. 2015, Gibert 2016).

102 A major challenge is to replace the current unidimensional representation of dispersal  
103 with a multidimensional viewpoint built on multiple external and internal drivers. To date,  
104 most studies focus on how mean dispersal behaviors (leaving, moving, and settling) change  
105 after fragmentation, assuming that environmental conditions are homogeneous among  
106 patches. However, landscapes can be heterogeneous independent of fragmentation; by  
107 reducing movements, fragmentation will alter the heterogeneity in biotic and abiotic  
108 conditions experienced by individuals and lineages. We hypothesize that habitat  
109 fragmentation should reduce variability (at any one point in time) of conditions within  
110 patches, but increase variability among patches. Although this effect likely depends on the  
111 detailed characteristics of fragmentation and species traits (see below), fragmentation should  
112 at the least influence spatial structuring and ultimately divergence across all levels of  
113 biological organization, from metapopulations, to metacommunities, to even metaecosystems.  
114 We conjecture that one effect of fragmentation is greater heterogeneity in local selective  
115 pressures. Reduced movements weaken the spatial averaging of local conditions, and should  
116 alter the means and variances of traits under selection, and how those variances are partitioned  
117 across space. Because of strong covariances of dispersal behavior with multiple phenotypic  
118 traits (Clobert et al. 2009), the evolution of dispersal syndromes may be deeply driven by  
119 these changes. Dispersers' phenotypic specializations should evolve in response to conditions  
120 experienced at each of the three steps of dispersal: the local conditions inducing dispersal  
121 decisions; matrix characteristics over which individuals move; and, the conditions  
122 encountered during settlement (Clobert et al. 2009). Habitat fragmentation, by decreasing

123 connectivity, and effects on the kind of heterogeneity experienced by individuals, should  
124 shape evolution of dispersal syndromes across multiple spatial scales.

125         After considering the evolution of dispersal as a unidimensional trait, we present a  
126 multidimensional viewpoint on how fragmentation influences dispersal evolution (Fig. 1). We  
127 develop predictions for how habitat fragmentation should shape the mean and variance of  
128 phenotypic traits locally and globally, as well as change dispersal syndromes (Fig. 1) in  
129 relation to proximal causes (e.g. genetic and environmental factors, Fig. 2). Finally, we  
130 underscore the importance of considering trait variation, and changes in such variation, for  
131 understanding metapopulation functioning.

132

### 133 **Evolution of dispersal strategies in a fragmented landscape**

#### 134 *Direct effects of fragmentation features*

135         The dispersal phenotype that evolves is determined by the balance between benefits  
136 and costs. Dispersal provides the benefits of escaping: competition with kin and/or non-kin  
137 conspecifics (e.g. Aars and Ims 2000, Cote et al. 2007, Hauzy et al. 2007), inbreeding (e.g.  
138 Szulkin et al. 2013), and adverse abiotic and biotic conditions [e.g. food availability:  
139 (O'Sullivan et al. 2014), predation risk: (Hauzy et al. 2007, Baines et al. 2014, Bestion et al.  
140 2014), interspecific competition (Fronhofer et al. 2015)]. However, dispersal incurs multiple  
141 costs. While there are costs associated with emigration and settlement, such as the lack of  
142 social bonds or adaptation to local conditions after immigration, costs inflicted by transience  
143 across the matrix are likely particularly influential following fragmentation (Bonte et al.  
144 2012). Dispersing between habitat patches may cost considerable time and/or energy for a low  
145 likelihood of success. Most empirical and theoretical studies on dispersal in fragmented  
146 landscapes have thus focused on the effect of matrix suitability and habitat patch geometry



147 (e.g. distances among habitat patches, number, shape and aggregation of habitat patches)  
148 (Travis et al. 2012).

149 Intuitively, the first prediction from theory is that reduced dispersal should be selected  
150 for in fragmented landscapes due to the increased costs and risks of moving across  
151 fragmented landscapes (Olivieri and Gouyon 1997; Travis and Dytham 1999), and indeed this  
152 is often found in empirical studies. Reduced dispersal propensity and distance moved have  
153 been reported when fragmentation increases, due to increased inter-habitat distances or  
154 reduced matrix permeability (Dempster 1991, Lens and Dhondt 1994, Diffendorfer et al.  
155 1995, Matthysen and Currie 1996, Haddad 1999, Debinski and Holt 2000, Mennechez et al.  
156 2003, Schooley and Wiens 2004, Bonte et al. 2006, Schtickzelle et al. 2006, Smith and Batzli  
157 2006, Matter 2006, Cheptou et al. 2008, Bowler and Benton 2009, Ahlroth et al. 2010,  
158 Bergerot et al. 2012, Eycott et al. 2012, Banks and Lindenmayer 2014).

159 However, theoretical studies also highlight the potential for more complex  
160 relationships between dispersal and habitat fragmentation (Olivieri and Gouyon 1997, Gandon  
161 and Michalakis 1999, Travis and Dytham 1999, Heino et al. 2001, Ronce and Olivieri 2004,  
162 Travis et al. 2012). Model results suggest that on already highly fragmented landscapes,  
163 further habitat loss sometimes selects for higher dispersal. This occurs because of the  
164 increased benefits that dispersal provides, at the point where local patch extinctions become  
165 common. Increased habitat loss raises the cost of dispersal, but the benefits gained through  
166 dispersal enabling recolonizations can outweigh these additional costs (Olivieri et al. 1995,  
167 Gandon and Michalakis 1999, Travis and Dytham 1999). While direct empirical tests of this  
168 prediction are lacking, there are a few indirect tests (Williams et al. 2016; Schtickzelle et al.  
169 2006). A recent experimental study on *Arabidopsis thaliana* showed an impressive evolution  
170 for longer dispersal distance in highly fragmented system (Williams et al. 2016), while in the  
171 butterfly, *Procllossiana eunomia*, there was a twofold short-term evolutionary response to

172 increased fragmentation (Schtickzelle et al. 2006). Although the propensity of emigration was  
173 lower in highly fragmented landscapes, actual emigrants dispersed faster with straighter  
174 movements. This increased the probability that emigrants find another suitable habitat, and  
175 also decreased dispersal mortality. Importantly, these results emphasize that the two  
176 behavioral strategies may evolve in concert in fragmented landscapes, leading to nonlinear  
177 patterns of dispersal responses (Schtickzelle et al. 2006).

178       Species can also evolve dispersal polymorphisms (e.g. sharp phenotypic distinctions  
179 between short- and long-distance dispersers) in response to increasing fragmentation.  
180 Theoretical studies predict that short and long distance dispersal strategies can emerge and  
181 coexist for moderate degrees of fragmentation, with frequencies varying with local conditions  
182 (Mathias et al. 2001, Hanski et al. 2004, Bonte et al. 2010, Hovestadt et al. 2011). For  
183 example, a clumped distribution of habitats can favor short-distance dispersal over long-  
184 distance dispersal (Mathias et al. 2001, Bonte et al. 2010). Empirical examples demonstrate  
185 that while long distance dispersal shrinks as habitat fragmentation increases, both strategies  
186 persist even under high fragmentation. In the weed *Crepis sancta*, long-distance dispersing  
187 seeds have a 55% lower chance of settling in a suitable patch within a fragmented urban  
188 environment (Cheptou et al. 2008). Following 5-12 generations of selection this dispersal cost  
189 resulted in a 4.5% reduction of long-distance dispersing seeds in fragmented habitats. In the  
190 dune wolf spider, *Pardosa monticola*, the percentage of spiderlings performing tiptoe  
191 behavior, a behavior inducing long-distance aerial dispersal, is negatively correlated with the  
192 degree of landscape fragmentation (Bonte et al. 2006). Notably, in both examples, long-  
193 distance dispersers persisted in fragmented landscapes (% long-distance dispersers in  
194 fragmented vs. continuous landscape: 85% vs. 89% in *Crepis sancta*, 4-6% vs. 14% in  
195 *Pardosa monticola*), suggesting that the two strategies stably coexist.

196 Habitat selection behaviors should also be selected in fragmented landscapes and  
197 likewise lead to mixed strategies. Such polymorphisms should be distributed between two  
198 extremes (Armsworth and Roughgarden 2005a): random dispersers, moving and settling  
199 independently of environmental conditions, and directed dispersers, who select patches that  
200 increase their expected fitness. In a spatially variable and temporally stable landscape, random  
201 dispersers endure the cost of moving away from suitable habitats to reach another habitat. In a  
202 highly fragmented environment, these costs may be particularly high. In temporally variable  
203 landscapes, random dispersers may however benefit from a bet-hedging strategy and the  
204 colonization of empty habitats (Armsworth and Roughgarden 2005b). Directed and  
205 conditional dispersers can track environmental conditions and avoid the cost of moving away  
206 from suitable habitats (Armsworth and Roughgarden 2005b). Although directed dispersers  
207 endure dispersal costs less often (e.g., following environmental changes), they likely suffer  
208 from the additional costs of gathering enough information (Stamps 2001) and of relying on  
209 potentially inaccurate information (Hale and Swearer 2016). Given the increased costs that  
210 random dispersers incur as habitat begins to fragment, we might expect to see an initial  
211 decrease in the frequency of random dispersers, for increasing habitat loss. However, as these  
212 random dispersers likely provide benefits in terms of recolonizing distant empty patches, we  
213 also predict that at higher levels of fragmentation, their frequency will increase with  
214 additional fragmentation. Importantly, the evolution of strategies at different dispersal phases  
215 are not independent; the evolution of movement and settlement strategies is likely to feedback  
216 on the evolution of emigration behavior (Travis et al. 2012).

#### 217 *Effects of fragmentation through a modification of local conditions*

218 Landscape fragmentation effects more than connectivity (Fahrig 2003), including  
219 changing habitat and population characteristics locally and globally. The relative influence on  
220 dispersal of different fragmentation effects is rarely considered (but see e.g. Delattre et al.

221 2013), with the notable exception of patch quality and size (e.g. Andreassen et al. 1998,  
222 Matter 2006, Bowler and Benton 2009, Baguette et al. 2011, Rémy et al. 2011). Because  
223 changes in patch size or quality often occurs as a function of landscape fragmentation, it is  
224 important to disentangle their relative influences on both biodiversity (Haddad et al. in press,  
225 Fahrig 2013) and dispersal evolution (Travis and Dytham 1999, North et al. 2011). An  
226 important consequence of reduced patch size and quality is reduced population size (North et  
227 al. 2011), accompanied by increasing demographic stochasticity, kin competition and  
228 inbreeding (Banks et al. 2005, 2007, Keyghobadi 2007, North et al. 2011 but see Sumner  
229 2005). Increases in these three factors should all select for increased dispersal (Hamilton and  
230 May 1977, Perrin and Mazalov 2000, Ronce et al. 2000, Lambin et al. 2001, Cadet et al. 2003,  
231 Parvinen et al. 2003), particularly when fragmentation reduces local population size and  
232 connectivity (Heino et al. 2001, Mennechez et al. 2003, Cote and Clobert 2010, Bitume et al.  
233 2013, Kubisch et al. 2013). For example, reduced gene flow among patches may increase  
234 relatedness and kin competition within patches (Banks et al. 2005c, Keyghobadi 2007) which  
235 should drive evolution towards higher dispersal rates (Hamilton and May 1977, Perrin and  
236 Mazalov 2000, Ronce et al. 2000). This may be reinforced if rare immigrants are selected  
237 over more related resident mates (i.e. for inbreeding avoidance, Pusey and Wolf 1996).  
238 However, immigrants may in some cases avoided by sexual partners to prevent outbreeding  
239 depression (Pusey and Wolf 1996), reducing selection for increased dispersal. Despite these  
240 clear theoretical predictions, the influence of habitat/population size, kin competition, or  
241 relatedness are rarely teased apart from effects of fragmentation on connectivity (e.g. Matter  
242 2006, Ahlroth et al. 2010). In one interesting study, Banks and Lindenmayer (2014) assessed  
243 the degree to which the decisions of agile antechinus (*Antechinus agilis*) to emigrate and  
244 settle depended on relatedness and patch characteristics (size, quality and isolation). They

245 found that inbreeding avoidance was as important for emigration and immigration decisions  
246 as were patch isolation and inter-patch distances (Banks and Lindenmayer 2014).

247 In addition to changing patch sizes and thus local demography and genetic structure,  
248 landscape fragmentation may slice habitat into patches in a quite unpredictable way,  
249 consequently reducing variability of environmental conditions in local patches and increasing  
250 variability among patches. The increased spatial variation between patches together with  
251 increased temporal variation in local populations sizes due to higher demographic  
252 stochasticity (Lande et al. 2003) will exert selection on dispersal strategies (Gadgil 1971,  
253 Paradis 1998, Heino et al. 2001, Mathias et al. 2001). Although temporal and spatial  
254 variability are often predicted to select for and against dispersal respectively (Duputié and  
255 Massol 2013), the temporal and spatial scales of fluctuations (e.g. spatial and temporal  
256 autocorrelation), the frequency and magnitude of fluctuations, and the combination of  
257 temporal and spatial variations will determine the direction and speed of dispersal evolution  
258 (McPeck and Holt 1992, Travis 2001, Duputié and Massol 2013). Interestingly, different  
259 dispersal strategies are more likely to coexist when environmental conditions are both  
260 spatially and temporally variable (Cohen and Levin 1991, McPeck and Holt 1992, Mathias et  
261 al. 2001, Parvinen 2002, Massol et al. 2011). For example, dispersal polymorphism can result  
262 from disruptive selection in landscape with heterogeneous perturbation rates, carrying  
263 capacities and patch sizes (Parvinen 2002, Massol et al. 2011). There are currently few  
264 empirical studies assessing this theory by quantifying environmental fluctuations and their  
265 consequences for dispersal evolution. In one exception, an experimental approach using  
266 *Caenorhabditis elegans* showed that spatiotemporally variable conditions favor the evolution  
267 of increased dispersal propensity in a patchy environment (Friedenberg 2003).

268 In a highly fragmented environment, different local populations may experience  
269 distinctive ecological conditions, e.g. social structure (density, sex-ratio, and age structure),

270 predator/prey densities and diversities, abiotic conditions: these local conditions may  
271 contribute to driving dispersal behaviors; blurring predictions made simply from local patch  
272 size and connectivity alone. For example, resource availability and diversity may vary among  
273 patches, leading to increased emigration rate from a subset of patches through a plastic  
274 response (Benard and McCauley 2008). This conditional dispersal should also have  
275 consequences for habitat selection in a fragmented landscape. After leaving a patch, emigrants  
276 will search for the most suitable habitats and select habitats matching their phenotype (i.e.  
277 habitat matching, (Edelaar et al. 2008)), or their natal habitat (i.e. natal habitat preference  
278 induction, Davis and Stamps 2004) or lacking the environmental condition that induced  
279 emigration. The reduced within-patch variation and increased environmental heterogeneity  
280 among patches should make optimal habitat selection harder, leading to higher dispersal  
281 mortality, imperfect habitat selection, and/or the selection for improved detection skills.

282         The above predictions assume that fragmentation reduces within-patch variability, but  
283 increases among-patch heterogeneity. These effects should depend on characteristics of the  
284 landscape (e.g., degree of heterogeneity, spatial autocorrelation), of the fragmentation (e.g.,  
285 degree of isolation, patch size), and of the focal species (e.g., movement abilities and  
286 occurrence). Edge effects, a common by-product of fragmentation, may increase  
287 environmental variability within patches. Several abiotic factors (e.g. light, temperature) and  
288 biotic factors (e.g. species composition, population density) are altered at patch borders  
289 (Murcia 1995). However, when patches are sufficiently small, effectively the whole patch is  
290 edge and then in within patch variability will match that of the matrix.

291         Regardless of the exact nature of changes, fragmentation will directly and indirectly  
292 act on the evolution of dispersal strategies, inducing a diversification of unconditional and  
293 conditional dispersal strategies. We suggest that the evolution of dispersal strategies in  
294 fragmented landscapes can only be understood from a multidimensional perspective

295 integrating those different phenotypic specializations (e.g. locomotor, competitive, orientation  
296 skills) that may covary with dispersal behavior at each of dispersal's three stages.

297

## 298 **Evolution of trait variance and covariance with dispersal strategies**

299

### 300 *Direct effects of fragmentation features*

301 Non-randomness of dispersal decisions results from the interaction between  
302 environmental context and individual phenotypes, at each of the three steps of dispersal  
303 (Edelaar and Bolnick 2012, Jacob et al. 2015). Individuals disperse in response to various  
304 local conditions (e.g. kin- and non-kin interactions, habitat quality, interspecific interactions),  
305 and not all individuals are equally influenced by these conditions (i.e. phenotypic attributes  
306 may shape an individual's expected success in diverse ecological conditions). This  
307 observation pertains to conditions encountered during transience and settlement. For instance,  
308 the ability to move across different landscapes may reflect a disperser's phenotype (e.g.  
309 locomotor and orientation skills), resulting in dispersal syndromes varying with dispersal  
310 costs and thus fragmentation features (level of fragmentation, but also matrix quality). In this  
311 section, we illustrate how landscape fragmentation may directly act on the evolution of  
312 dispersal syndromes (Fig. 1).

313 Impacts of fragmentation may act directly on phenotypic specializations of dispersers  
314 that facilitate movements across the landscape (Fig. 1, scenario 1, Table 1). Landscape  
315 fragmentation leads to increased distances among habitat patches. Depending on the degree of  
316 isolation, different dispersal strategies should be selected for (e.g. long-distance versus short-  
317 distance dispersers, directed versus random dispersers, active versus passive dispersers).  
318 These strategies represent a polymorphism in dispersal behaviors covarying with several  
319 phenotypic attributes related to enhancing and enabling traits.

320 In general, travelling longer distances and travelling across a fragmented landscape  
321 requires *enhancing traits* such as higher movement abilities and correlated phenotypic  
322 attributes, e.g., different metabolic fuels, muscle development (Zera and Denno 1997), body  
323 shape (Hill et al. 1999b), longer wings (Harrison 1980, Taylor and Merriam 1995, Zera and  
324 Denno 1997), longer legs (Trochet et al. 2016b) or better orientation and navigation skills  
325 (Vuilleumier and Perrin 2006, Merckx and Van Dyck 2007). For example, a recent study  
326 found larger eyes in dispersing than in philopatric individuals of the Bog Fritillary (*Boloria*  
327 *Eunomia*, Turlure et al. 2016). Interestingly, in the context of habitat fragmentation, the same  
328 study also found that the related Cranberry Fritillary, *Boloria aquilonaris*, a species that  
329 evolved within a naturally highly fragmented landscape, has larger eyes than the Bog  
330 Fritillary, suggesting that investments in physiology and morphology improving navigation  
331 may be selected under conditions of habitat fragmentation. Another study comparing  
332 populations of the silver-spotted skipper butterfly (*Hesperia comma*) showed that relative  
333 investment in thorax, a trait linked to flight ability, was higher for individuals in landscapes  
334 with patches further apart (Hill et al. 1999b). Phenotypic specialization improving long-  
335 distance dispersal may also be under selection in passively dispersed species, such as in  
336 *Arabidopsis thaliana* where highly fragmented systems conjointly select for greater height  
337 and dispersal distance (Williams et al. 2016).

338 Information gathering and processing abilities can be important enhancing traits,  
339 especially for individuals actively moving across complex landscapes and engaging in habitat  
340 matching. While we are not aware of studies comparing information processing skills between  
341 fragmented and continuous landscapes, comparisons have been made between long-distance  
342 and short-distance dispersers in the Siberian flying squirrel (*Pteromys volans* L.). Short-  
343 distance dispersers frequently revisited previously prospected sites to gather information and  
344 compare sites before making a settlement decision (Selonen and Hanski 2010). Long-distance



345 dispersers performed a sequential search, staying over a longer period of time in prospected  
346 sites without revisiting them. A possible explanation is the cost of revisiting sites when  
347 moving far from natal sites. A similar cost is likely to exist in fragmented landscape and we  
348 can expect a similar information processing and habitat selection strategy for dispersers in  
349 fragmented landscapes.

350 Long-distance dispersers can also display *enabling traits*, i.e. morphological structures  
351 or behaviors dedicated to the mode of dispersal (see above, e.g. wings in flying versus  
352 walking dispersers: Lombaert et al. 2006) and such traits might also be under selection in a  
353 fragmented landscape. For example, in several spider species, individuals may perform short-  
354 distance dispersal through walking or rappelling, or long-distance dispersal through  
355 ballooning or silk balls formation (Bonte et al. 2008, Clotuche et al. 2011). These strategies  
356 involve completely different behaviors and dispersal modes, as long-distance dispersers climb  
357 to a platform and perform tip-toe behavior or group themselves together in order to be  
358 passively dispersed by wind. The frequency of these dispersal strategies can vary with  
359 landscape fragmentation (Bonte et al. 2006) selection acts against individuals dispersed  
360 randomly over long-distance due to unpredictable wind currents.

361 Both *enhancing* and *enabling* dispersal traits can be costly to produce and may trade  
362 off against other life history traits. A recent meta-analysis showed that trade-offs between  
363 dispersal and other life-history traits occur across terrestrial and semi-terrestrial animals, but  
364 the nature and shapes of the relationships strongly vary among high taxonomic categories (i.e.  
365 orders, Stevens et al. 2014). In the wing-dimorphic field cricket (*Gryllus texensis*), long-  
366 winged males fly better than short-winged males, at the expense of higher aggressiveness and  
367 fighting propensity (Guerra and Pollack 2010), postponing access to reproduction (Zera and  
368 Denno 1997). Although reproductive penalties also exist in female wing dimorphic insects  
369 (Zera and Denno 1997), the nature and strength of dispersal syndromes is likely to vary by

370 sex (Hill et al. 1999a). For example, in the Bog Fritillary, there are sex differences in  
371 investment in the eye and, regardless of whether these are driven by differences in  
372 requirement for dispersal or are driven by requirements for better eyesight for another  
373 component of behavioral ecology (e.g. need to locate and identify host plants), it illustrates  
374 the importance of sex in dispersal syndromes. In male butterflies, for example, a high  
375 allocation to thorax may reflect mate location strategy (perching versus patrolling males)  
376 which might be linked to male dispersal or patch use in a fragmented landscape (Thomas et al.  
377 1998). Females and males may incur different dispersal costs, leading to sex-biased dispersal  
378 (Gros et al. 2008). Sex-biased dispersal can therefore evolve after landscape fragmentation if  
379 habitat isolation is more costly to female or male dispersers.

380       Habitat isolation is just one aspect of fragmentation and other biotic and abiotic  
381 characteristics of the landscape matrix may act on the evolution of covarying dispersal traits  
382 (Fig. 1, Table 1). For instance, higher predation risk is a dispersal cost in fragmented  
383 landscapes (e.g. Smith and Batzli 2006) and it might select for dispersers with a phenotype  
384 enhancing survival during movements. In common lizards (*Zootoca vivipara*), higher  
385 predation risk produces dispersers with a longer tail, a phenotype decreasing mortality from  
386 predation (Medel et al. 1988, Bestion et al. 2014).

### 387       *Effects of fragmentation through a modification of local conditions*

388       Fragmentation may result in narrower ranges of environmental conditions at the local  
389 patch scale and in variation among patches. These local conditions should select for dispersers  
390 with different phenotypes (*matching traits*, Fig. 1, scenarios 2 and 3, Table 1). Local  
391 conditions can affect dispersers' phenotypes in two different ways. First, local conditions may  
392 create patch-specific selective pressures and act as "plastic modifiers" of a suite of phenotypic  
393 traits, which alter dispersal propensities and dispersers' phenotypes (Fig. 1 scenario 2 and 3,  
394 Table 1). Dispersal could arise as a by-product of selection on other traits such as foraging

395 activity, mate location or the search for predation refuges (Benard and McCauley 2008,  
396 Burgess et al. 2016). Local conditions may thus select for increased (or decreased) foraging  
397 activity or predator avoidance strategies and indirectly modify dispersal propensity and  
398 disperser phenotypes. For instance, local predation risk induces important behavioral and  
399 morphological anti-predator adaptations (Agrawal et al. 1999, Verdolin 2006, Bestion et al.  
400 2014) altering individual departure from local habitat patches (Cronin et al. 2004, McCauley  
401 and Rowe 2010, Cote et al. 2013, Baines et al. 2014, Bestion et al. 2014). Among-patch  
402 variation in local predation risk may therefore create a phenotypic divergence between  
403 populations on different patches (Dingemanse et al. 2007, Bell et al. 2010); dispersers from  
404 populations with different local conditions (e.g. risk level) would carry different phenotypic  
405 adaptations even without any effect on a dispersal syndrome (Fig. 1 scenario 2, Table 1).  
406 Indeed, if all individuals (residents and dispersers) display these adaptations, covariation  
407 between dispersal and these adaptations may not necessarily vary with local predation risk.  
408 Such differences may also result from phenotypic plasticity, induced by developmental  
409 conditions, of traits related to dispersal capacity (reviewed in Benard and McCauley 2008).

410         Second, local conditions may change the covariance between dispersal decisions and  
411 other traits when locally less adapted individuals disperse to escape local conditions. Given  
412 that different phenotypes vary in their abilities to cope with different ecological factors (e.g.  
413 competition for food or mates, predation), the phenotype of individuals should shape the  
414 reaction to local conditions, producing context-dependent (i.e. conditional) dispersal  
415 syndromes (McPeck and Holt 1992, Cote and Clobert 2007a, Edelaar et al. 2008, Clobert et  
416 al. 2009). Context-dependent dispersal syndromes at the departure and settlement phases  
417 have been documented in several species (MacCallum et al. 1998, Byers 2000, Gilliam and  
418 Fraser 2001, Cote and Clobert 2007a, b, Bonte et al. 2008, Bolnick et al. 2009, Cote et al.  
419 2013, Maes et al. 2013, Pennekamp et al. 2014, Wey et al. 2015, Myles-Gonzalez et al. 2015,

420 Bestion et al. 2015b, Camacho et al. 2015, Jacob et al. 2016). For example, Pennekamp et al.  
421 (2014) investigated the role of genotype and environment interactions on dispersal propensity  
422 in a ciliate. They found marked differences in dispersal among genotypes, plasticity (in  
423 response to density) and evidence of genetic variability in this plastic response. This  
424 variability in plastic reaction norms likely reflects variability in aggregation behavior among  
425 genotypes (Jacob et al. 2016). After fragmentation, local populations may experience  
426 divergent external drivers of dispersal and exhibit different dispersal syndromes. We predict  
427 two major mechanisms for fragmentation to change dispersal syndromes through  
428 modifications of local conditions.

429 First, the degree and grain of environmental heterogeneity in the landscape, the degree  
430 of fragmentation, and patch size will determine the mean abiotic and biotic conditions within  
431 a patch. Given the multiplicity of dispersal drivers and of phenotypic traits correlated to  
432 dispersal, the external factors acting locally on emigration, phenotypic traits and their  
433 covariances are likely to vary across space (Fig. 1 scenario 3, Table 1), this dissimilarity  
434 increasing with inter-patch distance and patch size. For example, landscape fragmentation  
435 may change thermal conditions in patches due to the edge effect (Tuff et al. 2016). Small  
436 patches, with a high edge-to-interior ratio, may have warmer and less spatially variable  
437 climatic conditions. In common lizards, the thermal phenotypes of emigrants vary with the  
438 local thermal conditions (Bestion et al. 2015b). In warmer conditions, emigrants had lower  
439 thermal preferences at birth, and conversely, higher thermal preferences at birth when leaving  
440 cooler local conditions. Variability in patch size should thus induce variability in dispersers'  
441 thermal phenotypes. The realized variability in dispersal syndromes will depend on  
442 divergence of local conditions among patches resulting from fragmentation.

443 Second, fragmentation overlaying environmental heterogeneity should jointly shape  
444 the local diversity of conditions (Li and Reynolds 1995) and therefore the maintenance of

445 phenotypic diversity (Moran 1992). Less variable local conditions may reduce the local  
446 diversity of phenotypes with subsequent consequences for covariances between emigration  
447 behavior and phenotypic traits (Fig. 1 scenario 4, Table 1). Continuing our previous example,  
448 fragmentation-induced homogenization of climatic conditions for warmer conditions may  
449 select against individuals with cooler thermal optimum (Huey et al. 2012), reducing among-  
450 individual variation in thermal optimum and the potential for covariation with emigration  
451 behavior. These predictions illustrate how multiple environmental changes can modify the  
452 covariance of emigration with other traits from no covariation to covariations in opposite  
453 directions among patches.

454 Changes in local conditions may also affect covariation between *matching traits* and  
455 settlement decisions. Conditional immigration decisions should mirror conditional emigration  
456 decisions; for example, individuals leaving high density population should settle in low  
457 density populations (Cote and Clobert 2007a). Traits linked to emigration decisions should  
458 also be linked to habitat preference. For example, in three-spine stickleback (*Gasterosteus*  
459 *aculeatus*), stream and lake individuals morphologically differ (Bolnick et al. 2009). A  
460 transplant experiment showed that, while most fish returned to their native habitats, stream  
461 fish moving into the lake were morphologically similar to lake fish (and conversely) (Bolnick  
462 et al. 2009). Phenotype-dependent habitat preferences may therefore reinforce phenotypic and  
463 genotypic divergences among demes of a spatially-structured population (MacCallum et al.  
464 1998, Bolnick et al. 2009). Higher among-patch variation in environmental conditions may  
465 also select for dispersers with improved skills to process and memorize private and social  
466 information acquired while prospecting across the landscape. Such skills would help maintain  
467 the accuracy and efficiency of habitat selection while dispersing across a risky landscape.  
468 Overall, landscape fragmentation may change the covariance of dispersal strategies with other  
469 phenotypic traits directly or indirectly through modifications of local conditions.

470           Although there are many complexities, two major predictions emerge about how  
471 dispersal should evolve in fragmented landscapes: there should be diversification of  
472 unconditional dispersal strategies, and the sharpening of conditional dispersal strategies. The  
473 first prediction emerges from the non-monotonic costs-benefits balance of dispersal in  
474 fragmented landscapes (direct effects of fragmentation), and from the increased  
475 spatiotemporal variation at a local scale (indirect effects of fragmentation). Dispersal  
476 polymorphisms will likely span a resident strategy and a “super-disperser” strategy (Baguette  
477 and Van Dyck 2007), creating a continuous suite of dispersal strategies varying for *enabling*  
478 and *enhancing traits* (e.g. moving and orientation abilities). The second prediction emerges  
479 from the divergence of local dispersal drivers among patches (indirect effects of  
480 fragmentation), inducing context-dependent dispersal decisions and syndromes, i.e.  
481 conditional dispersal syndromes. While dispersal polymorphisms and conditional dispersal  
482 are both predicted to evolve in patchy environments (Cohen and Levin 1991, McPeck and  
483 Holt 1992), we believe that examining dispersers’ phenotypic traits may help reconcile these  
484 two predictions, and in particular the proximate pathways connecting dispersal behavior to  
485 other phenotypic traits.

486

#### 487 **Proximal causes of dispersal syndromes and their evolution along fragmentation** 488 **gradients**

489           Dispersal syndromes can arise from genes (G), environment (E) and G x E interactions  
490 (Langellotto et al. 2000, Cote et al. 2010, Shine et al. 2011, Ronce and Clobert 2012, Ducatez  
491 et al. 2012). To explore these pathways, we need to disentangle the determinants of dispersal,  
492 related *enabling, enhancing and matching* traits and their covariations.

493           The proximal causes of dispersal behavior have become a central focus of dispersal  
494 studies (Zera and Brisson 2012). Dispersal behavior has both genetic and environmental

495 determinants (Li and Margolies 1993, Pasinelli et al. 2004, Braendle et al. 2006, Sinervo et al.  
496 2006, Tschirren et al. 2007, Zera and Brisson 2012, Pennekamp et al. 2014). Traditionally,  
497 dispersal studies aimed to identify environmental determinants of dispersal (Clobert et al.  
498 2001), for instance in conditional dispersal. A growing number of studies now demonstrate a  
499 significant heritability of dispersal behavior and the major influence of several candidate  
500 genes has now been reported (Zera and Brisson 2012). The phenotypic traits covarying with  
501 dispersal behavior are also likely to be both genetically and environmentally determined  
502 (Trefilov et al. 2000, Gloria-Soria and Azevedo 2008, Niitepold et al. 2009, Duckworth and  
503 Sockman 2012, Korsten et al. 2013, Edelsparre et al. 2014), although the multiplicity of  
504 candidate traits and the types of covariation (*enabling*, *enhancing*, *matching* covariations)  
505 make generalization difficult.

506         The proximal causes of covariances between dispersal and other traits are more  
507 complex than either genes or the environment, alone (Cote et al. 2010, Ronce and Clobert  
508 2012). These covariations can result from immutable associations between dispersal behavior  
509 and phenotypic traits as predicted for *enabling traits*. The presence of *enabling traits* (e.g.  
510 wings) conditions dispersal (e.g. dispersal vs residency, long- vs short-distance dispersal). The  
511 proximal causes of covariations thus depend on the proximal causes of the traits involved.  
512 *Enabling traits* often have an important genetic and epigenetic determinism and so should  
513 their covariations with dispersal. Landscape fragmentation and local conditions should thus  
514 constitute selective pressures acting on the different dispersal morphs and change the  
515 proportion of dispersal strategies locally and across the landscape.

516         Second, dispersal syndromes can evolve in response to dispersal costs as predicted for  
517 *enhancing traits*. For example, dispersers with enhanced locomotor or orientation skills will  
518 better survive dispersal, especially in fragmented landscapes, than dispersers with poorer  
519 skills, leading to the evolution of dispersal syndromes. The evolution of dispersal syndromes

520 could be accelerated by diverse processes such as assortative mating in colonized habitats or  
521 at invasion fronts (Shine et al. 2011). These covariations are predicted to have an important  
522 genetic and epigenetic determinism and can arise from genes with pleiotropic effects or from  
523 linkage disequilibrium between genes involved in the two covarying traits. For example, in  
524 western bluebird (*Sialia mexicana*), aggression and dispersal are phenotypically and  
525 genetically correlated; while the integration of aggressiveness and dispersal is coordinated by  
526 shared genes, the actual strategy that emerges also depends on environmental variation  
527 (Duckworth 2009, Duckworth and Kruuk 2009). The strength of dispersal costs may not  
528 necessarily change the occurrence of dispersal strategies, but instead adjust the strength of  
529 associations between dispersal strategies and *enhancing traits*. As predicted for the direct  
530 effect of fragmentation, a polymorphism in dispersal strategies may be maintained through  
531 disruptive selection for skills dedicated to the different strategies.

532 Third, local environmental conditions can influence the strength and the direction of  
533 covariations between dispersal behavior and other phenotypic traits (i.e. *matching traits*),  
534 resulting in the labile expression of dispersal syndromes. Benard and McCauley (2008)  
535 suggested that local conditions may shape the phenotypic skills needed to disperse (i.e.  
536 dispersal capacity) and the motivation to disperse (i.e. dispersal propensity) resulting in  
537 covariation between phenotypic traits and dispersal behavior. For example, in a damselfly  
538 (*Enallagma boreale*), high-quality habitats produce larger individuals at emergence and, as  
539 body size is positively related to dispersal abilities, these habitats produce better dispersing  
540 individuals (Anholt 1990). However, a phenotype-dispersal covariance can only arise locally  
541 when some individuals change jointly their dispersal tendency and other traits, while others  
542 do not. Inter-individual variation can result from individuals experiencing locally different  
543 environmental conditions or from individual variation in “sensitivities” to environmental  
544 conditions reflecting complex environment-phenotype-genotype interactions (Baguette et al.



2015) acting on dispersal capacity and propensity. We suggest that individual variation in sensitivities may be important and that dispersal can be a behavioral response to ‘excitabilities’ (i.e. sensitivities) to different environmental stimuli (Fig. 2). A suite of *matching traits*, genetically and environmentally determined, could underlie individuals’ excitability to environmental conditions and whether individuals would react “negatively” to local conditions or not. An individual would disperse away from local conditions rather than opt for another stressors avoidance strategy (e.g. hiding in a predator context, submissive behavior in a competition context, Dantzer 1989, Koolhaas et al. 1999) depending on its dispersal capacity. This dispersal capacity would result from a suite of *enabling* and *enhancing traits*. This framework differentiates two categories of phenotype-dispersal associations.

The first compiles phenotypic traits (i.e. *enabling* and *enhancing traits*) that are linked to dispersal capacity (e.g. locomotor skills). Such covariations with dispersal behavior (i) would vary in strength, not in direction (e.g. dispersers have similar or better, but not worse, locomotor skills than residents); (ii) would have a significant genetic determinism and; (iii) would have a strong potential to evolve in a fragmented landscape towards a polymorphism of dispersal strategies. These phenotypic specializations would therefore be carried by most dispersers.

The second category groups together phenotypic traits (i.e. *matching traits*) that appear genetically uncoupled from dispersal. These traits (i) can covary positively, negatively or not with dispersal behavior depending on local conditions. Their covariations with dispersal behavior are (ii) less likely genetically determined and; (iii) in a fragmented landscape, should reflect the evolution of conditional dispersal. Excitability to certain environmental conditions, leading to emigration or other risk avoidance behavior, could genetically covary with phenotypic traits. Dispersers would display these phenotypic

570 attributes in a context-specific manner, as dispersal would be indivisible from its local  
571 dispersal inducer (density-dependent dispersal, predator-dependent dispersal, kin competition  
572 dependent-dispersal and so on).

573 Although this framework requires theoretical enrichment and empirical  
574 demonstrations, this classification could conciliate 1) the evolution of dispersal  
575 polymorphisms and conditional dispersal in fragmented landscapes and 2) the genetic  
576 determinism and the context dependency of syndromes. By altering dispersers' attributes,  
577 landscape fragmentation should modify gene flow between patches. Conditional and  
578 unconditional dispersal syndromes only exist because some individuals more readily disperse  
579 in response to landscape features and local conditions. It is likely that a single gene underlies  
580 such inter-individual variation in dispersal response, related phenotypic traits, or excitability.  
581 Modified dispersal syndromes should therefore lead to non-random gene flows in a  
582 metapopulation with potential consequences on its dynamics (Jacob et al. 2015).

583

#### 584 **Consequences for spatially-structured populations**

585 A better understanding of the evolution of dispersal syndromes and its consequences  
586 requires discussing how dispersal syndromes may vary across ecological and spatial scales.  
587 We predict that an unsuitable and risky matrix, coupled with increased spatiotemporal  
588 variation, should lead to the evolution of diverse strategies including emigration, transience  
589 and settlement decisions. Distributed between a resident strategy and a “super-disperser”  
590 strategy, these strategies would covary with a suite of phenotypic specializations. Abiotic and  
591 biotic conditions in the matrix shape the selective pressures acting on the ability of dispersers  
592 to successfully cross the matrix. We expect the evolution of a general dispersal syndrome at  
593 the metapopulation scale, but with local variation. For example, patch clumping can induce  
594 looser associations between dispersal behavior and moving ability locally, altering the

595 dispersal syndrome across the entire metapopulation. The evolution of a dispersal  
596 polymorphism should improve metapopulation persistence, because only individuals with a  
597 dedicated phenotype should attempt to cross the matrix, increasing the success of movements  
598 among local populations and likely homogenizing local populations in a landscape. Aside  
599 from moving skills, these strategies should co-evolve with other traits, especially  
600 habitat/resource specialization (Kisdi 2002, Ravigné et al. 2009, Nurmi and Parvinen 2011).  
601 Although individuals with low dispersal are predicted to be habitat specialists (Kisdi 2002,  
602 Nurmi and Parvinen 2011), the degree of habitat specialization in dispersers will depend on  
603 the rules for habitat choice (Ravigné et al. 2009) and landscape features. For example, random  
604 dispersers should likely be habitat generalists, while directed dispersers should display some  
605 degree of specialization.

606         A second set of predictions relates to increased heterogeneity in local conditions  
607 among patches. We might expect no general dispersal syndrome at the metapopulation scale,  
608 but a diversity of syndromes tailored to local conditions. A diversity of dispersal syndromes  
609 can be maintained in a metapopulation because of habitat matching (Edelaar et al. 2008, Jacob  
610 et al. 2015). In a fragmented, heterogeneous landscape, dispersers will benefit from selecting  
611 local patches that better match their phenotypes. As proximal causes of dispersal capacity and  
612 environmental excitability are uncoupled in our framework, the settlers can propagate their  
613 dispersal capacity genes and allow individuals of the next generation to disperse when they  
614 are less adapted to local conditions (i.e. high excitability). This non-random gene flow could  
615 hasten local adaptation and population differentiation at the metapopulation scale (Edelaar et  
616 al. 2008, Jacob et al. 2015 but see Holt and Barfield 2015). However, habitat matching  
617 requires dispersers to prospect different habitat patches before settling and therefore they  
618 might incur higher dispersal costs especially in hostile matrices. Habitat matching could  
619 enhance the adaptiveness of gene flow at the expense of immigration rates. Merging the first

620 set of predictions with this one, we expect evolution towards both efficient dispersal and  
621 habitat matching, which would result in the fastest local adaptation and population  
622 differentiation in a metapopulation.

623         Predicting the persistence and dynamics of spatially-structured populations is a major  
624 goal for contemporary ecologists and evolutionary biologists, especially given rapid  
625 environmental changes. An improved ability to forecast species' responses to environmental  
626 changes (Urban et al. 2016) requires precise estimates of the mean and variance of species  
627 dispersal among patches and, for a local patch, the balance between the mean and the variance  
628 of emigration and immigration rates. Many models now just assume that an immigrant equals  
629 an emigrant and that dispersal asymmetry results from unbalanced rates. However, this may  
630 not be valid when considering covariances between individuals' dispersal and functional  
631 traits. Immigrants may display a totally different set of phenotypic traits than emigrants, and  
632 asymmetric dispersal can result from the phenotypic composition of immigrant and emigrant  
633 pools (Benard and McCauley 2008). In such a situation, the emigration-immigration balance  
634 is harder to gauge. As contrasted dispersal phenotypes might have different fitness in different  
635 patches, phenotype-dependent emigration and immigration decisions could influence source-  
636 sink dynamics and the speed of adaptation in spatially-structured populations (Holt and  
637 Barfield 2015). How such differences might impact dynamics is a key question with  
638 important consequences. Consider sex-biased dispersal. Local conditions, such as local  
639 competition, predation risk or inbreeding, as well as spatiotemporal variability, may lead to a  
640 pool of dispersers with a biased sex-ratio if males and females suffer differently from these  
641 conditions (Gros et al. 2008, Henry et al. 2016, Trochet et al. 2016a). In a fragmented and  
642 heterogeneous landscape, some patches may experience female-biased emigration and male-  
643 biased immigration. Emigration and immigration might seem balanced at first glance, but this  
644 asymmetry could strongly bias sex-ratio and endanger population persistence (Le Galliard et

645 al. 2005a). By neglecting dispersal syndromes, we might underestimate the impacts of  
646 fragmentation on population and community persistence. Overall dispersal distances and rates  
647 might not be changed by landscape fragmentation, even while some dispersal syndromes  
648 disappear or emerge, causing cryptic changes in functional biodiversity within  
649 metapopulations and metacommunities (Stevens et al. 2014). Below we provide a few  
650 promising future directions for incorporating the multidimensionality of dispersal syndromes  
651 into studies predicting and quantifying the consequences of fragmentation.

652

653 **Developing theory on the causes and consequences of dispersal syndromes in**  
654 **fragmented landscapes - key challenges**

655 Modeling frameworks are now available for exploration of the joint evolution of traits at each  
656 of the three stages of dispersal, but have not yet been used to gain a general understanding of  
657 how emigration, transfer and settlement rules/behaviors jointly evolve as a function of the  
658 degree and spatial pattern of habitat fragmentation. A priority should be to develop a general  
659 understanding of the interplay between the evolution of behaviors for each stage under a  
660 broad range of environmental conditions. For example, it would be relatively straightforward  
661 to apply existing methods (Travis et al. 2012, Bocedi et al. 2014) to determine under what  
662 range of life histories, and for which spatial environmental configurations we might expect  
663 evolution of a dispersal strategy comprising low emigration rate together with high distance  
664 (and high risk) transfer. It is particularly important to understand which species' life history  
665 characteristics and fragmentation attributes lead to dispersal evolution improving population  
666 persistence), and when it leads to negative impacts, including the potential for evolutionary  
667 suicide (Delgado et al. 2011). While we have a reasonable understanding of these effects for  
668 the evolution of emigration rates (Delgado et al. 2011), there appear to be no studies that

669 consider how the balance between positive and negative effects changes for more complex  
670 dispersal syndromes.

671 A further priority is developing models that allows for dispersal (at the three stages) to  
672 coevolve with other life history characteristics and phenotypic traits. A few models do  
673 incorporate trade-offs between dispersal and competitive ability, reproductive ability, and/or  
674 habitat specialization (e.g. Burton et al. 2010, Nurmi and Parvinen 2011) but these typically  
675 model dispersal in a rather simple way (Burton et al. 2010, Nurmi and Parvinen 2011). The  
676 priority now, given the urgent need for modeling that yields quantitative ecological  
677 forecasting predictions (Evans 2012, Evans et al. 2012, Urban et al. 2016), is to allow  
678 covariances between dispersal traits and other phenotypic and life history traits to emerge  
679 from a more biologically realistic model. This requires incorporation of physiological costs  
680 that properly represent trade-offs between, for example, investment in larger eyes to improve  
681 navigation and fecundity. It is also critical to recognize and account for the fact that not all  
682 dispersal traits are solely for dispersal (Benard and McCauley 2008, Burgess et al. 2016). For  
683 example, navigation capability gained by having larger eyes may under some conditions  
684 become less important for dispersal. However, if this visual capability remains critical for  
685 foraging efficiency, finding mates or avoiding predators, it will not necessarily be the case  
686 that investment in eye size can be traded off to gain, for example, greater fecundity. These  
687 constraints are not currently embedded within models focused on dispersal. A further key  
688 issue is to ascertain the genetic basis for the covariances between the traits that make up a  
689 dispersal syndrome. In particular, the *enabling*, *enhancing* and *matching* framework entails  
690 assessing both genetic and plastic components of phenotypic covariances. The manipulation  
691 of environmental variability and of landscape features would allow predictions of the  
692 emergence of different trait associations in dispersers. Developing a quantitative genetic  
693 and/or explicit genetic framework for modeling dispersal syndromes is essential for better

694 understanding of dispersal evolution in fragmented landscapes and assessing how such  
695 evolution impacts population dynamics (see also Legrand et al. in press).

696

### 697 **Advancing the empirical evidence for dispersal evolution in fragmented landscapes**

698 We need to better understand both proximal and ultimate causes of dispersal behaviors  
699 and syndromes, which is challenging for dispersal syndromes and their conditionality. How  
700 can labile dispersal syndromes concord with heritable dispersal behavior and with the few  
701 reported genetic covariances with phenotypic traits? To answer this question, empiricists need  
702 first to quantify covariation between the phenotype and dispersal behaviors. This requires  
703 targeting a suite of phenotypic traits that can depict different functions linked to movements  
704 (e.g. locomotion, orientation) and to dispersal drivers (e.g. sexual secondary characters,  
705 competitive and social abilities) and monitoring their covariation with emigration, transience  
706 and immigration behaviors. A related step is to apply reaction norms techniques (Martin et al.  
707 2011) to quantify variation of dispersal syndromes with a suite of ecological conditions (e.g.  
708 population density, sex-ratio, community composition). This task can be done at two temporal  
709 scales: a short-time scale to measure plastic reaction norms, and, a longer time scale, to  
710 quantify evolved dispersal syndromes (e.g. for unicellular organisms see Pennekamp et al.  
711 2014, Jacob et al. 2016) and quantify the selection for covariation in different contexts.  
712 Combining these studies with functional genetics would allow disentangling the respective  
713 and interactive influences of genome, epigenome and phenome on dispersal behaviors and  
714 syndromes (Baguette et al. 2015). We expect some phenotypic traits to monotonously and  
715 genetically covary with dispersal decisions (*enabling* and *enhancing traits*), while *matching*  
716 *traits* would contextually covary with dispersal behaviors. Genetic covariations could only be  
717 tracked down after controlling for the multiple drivers of dispersal. The estimation of genetic

718 covariations would allow dismantling the proximal causes of dispersal capacity and of  
719 excitability to environment stimuli.

720         Second, our framework may help identify key fragmentation features that influence  
721 dispersal behaviors and syndrome and therefore help empiricists distinguish wide-spread from  
722 case-specific effects. Following recommendations from theorists (Martin and Fahrig 2015),  
723 we should empirically study the relative influence of matrix quality, patch size, patch isolation  
724 and edge effects on dispersal behaviors, phenotypic traits and their covariances. More  
725 information on within- and among-patch variation in conditions may be particularly important  
726 to quantify. This is empirically challenging, but we recommend going beyond quantifying  
727 emigration and immigration in continuous and fragmented landscapes to assess underlying  
728 suites of key traits. These traits can have ecological consequences as important as the number  
729 of dispersers (e.g. in disease spread, predation strength). These data can also help  
730 experimenters to design novel experimental landscapes. Experimental semi-natural systems  
731 (Resasco et al. in press, Debinski and Holt 2000, Legrand et al. 2012, Altermatt et al. 2015,  
732 Haddad et al. 2015) have much to offer in this respect, in particular to disentangle plastic from  
733 selective effects of habitat features. Joint theoretical and experimental studies should further  
734 quantify how the evolution of various dispersal syndromes alters gene flow under different  
735 environmental contexts. Ascertaining whether fragmentation driven selection on dispersal  
736 syndromes leads to adaptive trait covariations and dispersal decisions, or instead modifies  
737 patterns of traits covariation so as that reduces fitness and/or effective gene flow is a central  
738 question for further research. Finally, semi-natural experiments offer the possibility to study  
739 eco-evo feedbacks induced by landscape fragmentation (Legrand et al. in press), beyond  
740 evolution of dispersal syndrome. Accurate predictions of biodiversity futures require the  
741 implementation of eco-evo feedback loops in empirical and theoretical studies.

742



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## 1237 **Figure legend**

1238 **Figure 1.** Direct (solid line, scenario 1) and indirect (dotted lines, scenario 2 and 3) impacts of  
1239 fragmentation features on the evolution of dispersal decisions, other phenotypic traits and  
1240 their covariances (i.e. dispersal syndromes). In scenario 1, habitat fragmentation directly acts  
1241 on dispersal propensities and distance moved by increasing dispersal costs. In addition,  
1242 fragmentation selects for dispersers with phenotypic specializations improving their abilities  
1243 to cross a matrix and travel longer distances (i.e. enabling and enhancing traits, e.g. wings  
1244 size, muscles, metabolic fuels). In scenarios 2 to 4, habitat fragmentation acts on the evolution  
1245 of dispersal decisions and syndromes through changes in the mean and variance of local  
1246 environmental conditions. Fragmentation creates a patchwork of habitats with different mean  
1247 local conditions at a global scale. Changes in mean local conditions (scenarios 2 and 3), such  
1248 as predation risk, population density or relatedness, may select for higher or lower dispersal  
1249 rates. These changes could also select for phenotypic attributes improving local adaptation  
1250 (i.e. matching traits). These changes do not necessarily modify covariations between dispersal  
1251 decisions and phenotypic traits if all individuals (dispersers and residents) display the  
1252 phenotypic adaptations (scenario 2). A modification of covariations can occur when  
1253 individuals less adapted locally disperse to escape local conditions (scenario 3). Covariations  
1254 may also be modified by a decrease in variance of local conditions and therefore the local  
1255 diversity of phenotypes (scenario 4).

1256 **Figure 2.** A scenario to explain context-dependent (aka conditional) dispersal syndromes.  
1257 Context-dependent dispersal syndromes refer to covariations between dispersal behavior and  
1258 phenotypic traits varying with local conditions. In this scenario, the two concepts in grey  
1259 boxes, *dispersal capacity* and the *excitability to environmental stimuli*, are driven by different  
1260 set of genes and environmental conditions and involve different types of traits (i.e. enabling,  
1261 enhancing and matching traits). Depending on their *excitability to different environmental*



1262 *stimuli*, individuals may react to local conditions and this reaction should covary with  
1263 matching traits. The type of reaction, dispersal or other avoidance strategies (e.g. hiding),  
1264 depend on *dispersal capacity* which depends on individuals' enabling and enhancing traits  
1265 (e.g. wing presence or size, muscles).

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**Table 1: Predicted effects of fragmentation on dispersal decision, on phenotypic traits and on their covariances (i.e. dispersal syndromes)**

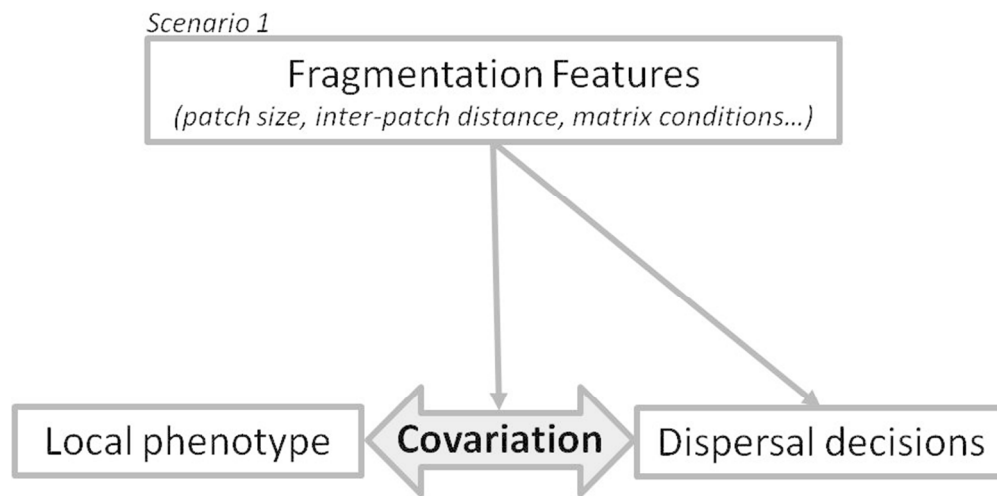
	<b>Environmental condition<sup>a</sup></b>	<b>Dispersal traits changed<sup>b</sup></b>	<b>Potential traits changed<sup>c</sup></b>	<b>Whose phenotype changed?<sup>d</sup> Are covariances changed?</b>	<b>Scenario (Fig. 1)<sup>e</sup></b>
<b>Landscape conditions</b>	Fragmentation level (+) Habitat Loss (+) Inter-patch distance (+) Matrix viscosity (+) Isolation (+)	Emigration prob. (-) <sup>3,4,6,7,8,10,11,12,13,14,15,19,22,27</sup> Emigration prob. (+) Distance moved (+) <sup>3,20,24,27</sup> Distance moved (-) <sup>8,9,18,19,24</sup> Dispersal timing (+) <sup>1,2</sup> Return prob. (+) Immigration prob. (-) <sup>1,2,6,7,10,12,13,22</sup> Transience success (-) <sup>6,7,10,11,12,23</sup>	Body size and shape (+) <sup>20,97,98</sup> Wing length and width (+) <sup>20</sup> Condition/energetic resources (+) Musculature/metabolism (+) <sup>24</sup> Mobility traits (+) <sup>20,24</sup> Mobility traits (-) <sup>4,5,7,9,24</sup> Locomotor endurance/ speed (+) <sup>16,17</sup> Boldness/Exploration(+) Orientation skills (+) <sup>25,26</sup> Movement straightness (+) <sup>6,16,17,21</sup>	Dispersers Covariance changed <sup>4,6</sup>	Scenario 1 (Adaptive disp. syndrome)
	Matrix risk level (+) (e.g. predation risk)	Emigration prob. (-) Distance moved (-) Dispersal duration (-) Return prob. (+) Immigration prob. (-) Transience success (-) <sup>10,23</sup>	Body size/mass (-/+) Antipredator traits (+) Boldness (+) Locomotor speed (+) Movement straightness (+)	Dispersers Covariance changed <sup>4</sup>	Scenario 1 (Adaptive disp. syndrome)
	Matrix resources level (-)	Emigration prob. (-) Distance moved (-) Dispersal duration (-) Return prob. (+) Immigration prob. (-) Transience success (-)	Body size (-) Condition/energetic resources (+) Locomotor speed (+) Locomotor endurance (+) Movement straightness (+)	Dispersers Covariance changed <sup>4</sup>	Scenario 1 (Adaptive disp. syndrome)

This table reports predictions for effects of fragmentation on dispersal traits. Fragmentation features can act directly on dispersal and related phenotypic traits (scenario 1 in Fig. 1) or can act indirectly through modifications of the mean (scenario 2-3 in Fig. 1) and the variance (scenario 4 in Fig. 1) of local conditions. We first report environmental conditions that can be changed by fragmentation at the landscape or local scales (a). The sign +/- describes an increase or a decrease of this condition (a) and the direction of predictions on changes in dispersal traits (b) and phenotypic traits (c). We further report in (d) whether we expect the phenotypic traits (c) to change in dispersers, residents or in similar intensity in residents than dispersers (Residents = Dispersers) or not (Residents > Dispersers). It should therefore result into changes of covariances between dispersal and phenotypic traits or not (d). We finally associate these predictions with scenarios in Fig. 1.

	Environmental condition <sup>a</sup>	Dispersal traits changed <sup>b</sup>	Potential traits changed <sup>c</sup>	Whose phenotype changed? <sup>d</sup> Are covariances changed?	Scenario (Fig. 1) <sup>e</sup>
<b>Local conditions</b>	Predation risk (+)	Emigration prob. (+) <sup>28,29,36,37,40,89</sup> Distance moved (+) <sup>38,40</sup> Immigration prob. (-) <sup>41</sup>	Body size/shape (+) <sup>28,35,39</sup> Antipredator traits (+) <sup>28,31</sup> Boldness/Exploration (-) <sup>34</sup> Activity (-) <sup>30,32</sup> Activity (+) <sup>28</sup> Social behavior (+) <sup>33</sup> Aggressiveness (+) <sup>31</sup> Locomotor speed (+) <sup>35</sup> Stress level (+) <sup>31</sup>	Residents=Dispersers Covariance unchanged <sup>36</sup>  Residents> Dispersers Covariance changed <sup>28,29,40</sup>	Scenario 2 (Random dispersal)  Scenario 3 (Habitat matching)
	Density (+) Competition (+) Food availability (-)	Emigration prob. (-) <sup>10,42,43,44,45</sup> Immigration prob. (-) <sup>10,42</sup> Emigration prob. (+) <sup>37,42,43,47,48,54,89</sup> Immigration prob. (+) <sup>42</sup> Distance moved (+) <sup>46</sup> Dispersal timing (-) <sup>51,52</sup> Dispersal duration (-) <sup>51</sup>	Body size (-) <sup>49,53,55,56</sup> Energy requirement/metabol.(-) <sup>56</sup> Activity (+) <sup>50,55</sup> Competitive/fighting skills (+) <sup>57</sup> Social behavior (+) <sup>42,50</sup> Foraging activity (-/+) <sup>54</sup> Diet specialization (+) <sup>58,59</sup>	Residents=Dispersers Covariance unchanged <sup>44,52</sup>  Residents> Dispersers Covariance changed <sup>42,43,45,48,51</sup>	Scenario 2 (Random dispersal)  Scenario 3 (Habitat matching)
	Sex ratio (more males) Density of males (+) Density of females (-)	Emigration prob. (-/+) <sup>60</sup> Immigration prob. (-/+) <sup>60</sup> Transience success(-/+) <sup>60</sup> Sex-biased dispersal (+) <sup>61,62,63</sup>	♂/♀ body size/mass (-/+) <sup>64,68</sup> ♂ fight skills (+) <sup>65</sup> ♂ secondary sexual character (+) <sup>66</sup> ♀ mate choosiness (+) <sup>64,66</sup> ♀ coercion avoidance skills (+) <sup>67</sup>	Residents=Dispersers Covariance unchanged  Residents> Dispersers Covariance changed <sup>60</sup>	Scenario 2 (Random dispersal)  Scenario 3 (Habitat matching)
	Relatedness (+) Kin Competition (+)	Emigration prob. (+) <sup>13,71</sup> Emigration prob. (+) <sup>71,72</sup> Immigration prob. (-) <sup>13</sup> Distance moved (+) <sup>46</sup> Sex-biased dispersal (-/+) <sup>73</sup>	Cooperation (+) <sup>69</sup> Mate choosiness (+) <sup>70</sup>	Residents=Dispersers Covariance unchanged <sup>73</sup>  Residents> Dispersers Covariance changed <sup>72</sup>	Scenario 2 (Random dispersal)  Scenario 3 (Habitat matching)

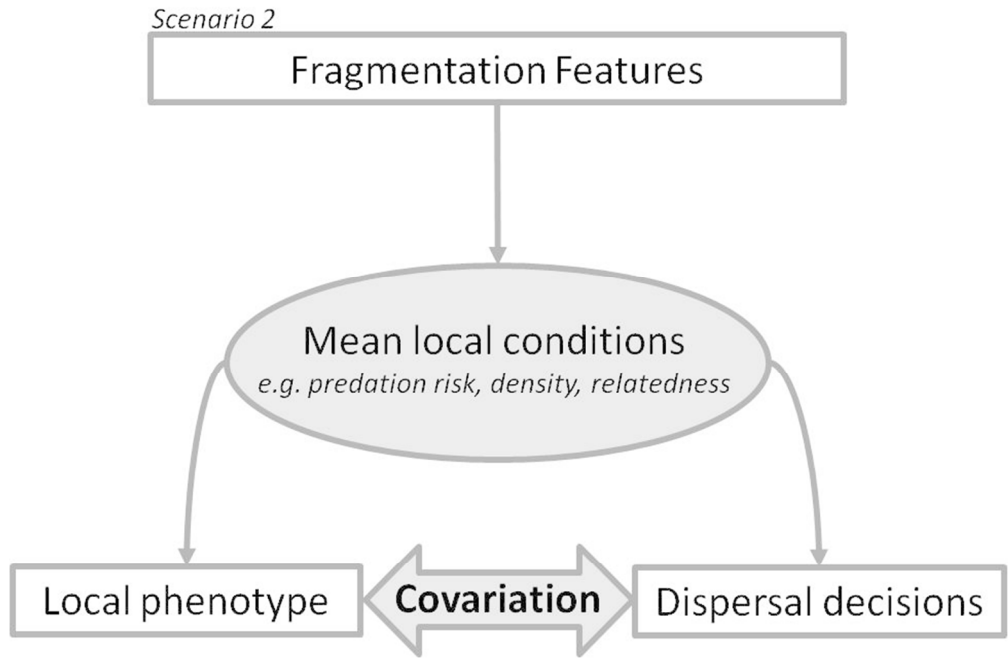
	<b>Environmental condition<sup>a</sup></b>	<b>Dispersal traits changed<sup>b</sup></b>	<b>Potential traits changed<sup>c</sup></b>	<b>Whose phenotype changed?<sup>d</sup> Are covariances changed?</b>	<b>Scenario (Fig. 1)<sup>e</sup></b>
	<u>Abiotic conditions:</u> Temperature/hygrometry Soils Topography Water level Wind speed/direction	Emigration prob. <sup>54,75,76,77,78</sup> Immigration prob. Distance moved <sup>74,75,79,80,40</sup>	Thermal physiology <sup>86</sup> Water balance <sup>83</sup> Stoichiometry <sup>85</sup> Physiology <sup>82,87</sup> Activity/movement <sup>54,79</sup> Body size/shape <sup>81,84,85</sup>	Residents=Dispersers Covariance unchanged  Residents> Dispersers Covariance changed <sup>77,80</sup>	Scenario 2 (Random dispersal)  Scenario 3 (Habitat matching)
	<u>Spatial heterogeneity of:</u> Predation risk (-) Food availability (-) Competition (-) Abiotic conditions (-)	Variance in emigration (-) Emigration prob. (+)	Variance in above traits (-) <sup>88</sup>	Residents=Dispersers Covariance removed	Scenario 4 (Phenotype monomorphism)
	Predator diversity (-) Prey diversity (-) Competitor diversity (-)	Emigration prob. (-) <sup>90,92</sup> Immigration prob. (+) <sup>91</sup> Distance moved (+) <sup>90</sup> Emigration prob. (+) <sup>90</sup>	Antipredator specialization (+) <sup>93</sup> Handling/Digestive specialization (-/+) <sup>94,95,96</sup> Diet specialization (-/+) <sup>94</sup>	Residents=Dispersers Covariance unchanged  Residents=Dispersers Covariance removed  Residents> Dispersers Covariance changed	Scenario 2 (Random dispersal)  Scenario 4 (Phenotype monomorphism)  Scenario 3 (Habitat matching)

Numbers refer to articles illustrating the effect of environmental conditions on dispersal traits (b) and on phenotypic traits (c). For (d), the references report effects of environmental conditions on covariances. 1: Lens and Dhondt 1994; 2: Matthysen and Currie 1996; 3: Mennechez et al. 2003; 4: Bonte et al. 2006; 5: Maes et al. 2013; 6: Schtickzelle et al. 2006; 7: Cheptou et al. 2008; 8: Ahlroth et al. 2010; 9: Bergerot et al. 2012; 10: Smith and Batzli 2006; 11: Matter 2006; 12: Bowler and Benton 2009; 13: Banks and Lindenmayer 2014; 14: Eycott et al. 2012; 15: Schultz and Crone 2001; 16: Stevens et al. 2005; 17: Goodwin and Fahrig 2002; 18: Schooley and Wiens 2004; 19: Merckx et al. 2003; 20: Taylor and Merriam 1995; 21: Schtickzelle et al. 2007; 22: Haddad 1999; 23: Matter et al. 2004; 24: Hanski et al. 2004; 25: Turlure et al. 2016; 26: Merckx and Van Dyck 2007; 27: Diffendorfer et al. 1995; 28: Bestion et al. 2014; 29: Cote et al. 2013; 30: Teyssier et al. 2014; 31: Bell et al. 2010; 32: Moses and Sih 1998; 33: Krause and Ruxton 2002; 34: Bell and Sih 2007; 35: Langerhans et al. 2004; 36: Baines et al. 2015; 37: Baines et al. 2014; 38: Hakkarainen et al. 2001; 39: Coslovsky and Richner 2011; 40: Gilliam and Fraser 2001; 41: Morris 2003; 42: Cote and Clobert 2007a; 43: Cote and Clobert 2007b; 44: Kuussaari et al. 1996; 45: Pennekamp et al. 2014; 46: Bitume et al. 2013; 47: Bagueette et al. 2011; 48: Byers 2000; 49: Einum et al. 2011; 50: Le Galliard et al. 2015; 51: Kim 2000; 52: Rémy et al. 2011; 53: Mugabo et al. 2010; 54: Tuda and Shima 2002; 55: Cote et al. 2008; 56: Bohlin et al. 1994; 57: Knell 2009; 58: Svanbäck and Persson 2004; 59: Evangelista et al. 2014; 60: Trochet et al. 2013; 61: Barros et al. 2013; 62: Sandell et al. 1990; 63: Steifetten and Dale 2011; 64: Dreiss et al. 2010; 65: Kvarnemo et al. 1995; 66: Jirotkul 1999; 67: Gossam et al. 2001; 68: Le Galliard et al. 2005b; 69: Ruch et al. 2009; 70: Blyton et al. 2016; 71: Cote et al. 2007; 72: Davis 2012; 73: Le Galliard et al. 2003; 74: Damschen et al. 2014; 75: Delattre et al. 2013; 76: Bestion et al. 2015b; 77: Legrand et al. 2015; 78: Bonte et al. 2007; 79: Kuefler and Haddad 2006; 80: Nitepold et al. 2009; 81: Sheridan and Bickford 2011; 82: Dillon et al. 2010; 83: Kearney et al. 2013; 84: Bestion et al. 2015a; 85: Norlin et al. 2016; 86: Huey et al. 2012; 87: Meylan et al. 2012; 88: Moran 1992; 89: Hauzy et al. 2007; 90: Fronhofer et al. 2015; 91: Binckley and Resetarits 2005; 92: Sih and Wooster 1994; 93: Relyea 2003; 94: Araújo et al. 2011; 95: Olsson et al. 2007; 96: Persson 1985; 97: Thomas et al. 1998; 98: Hill et al. 1999b.



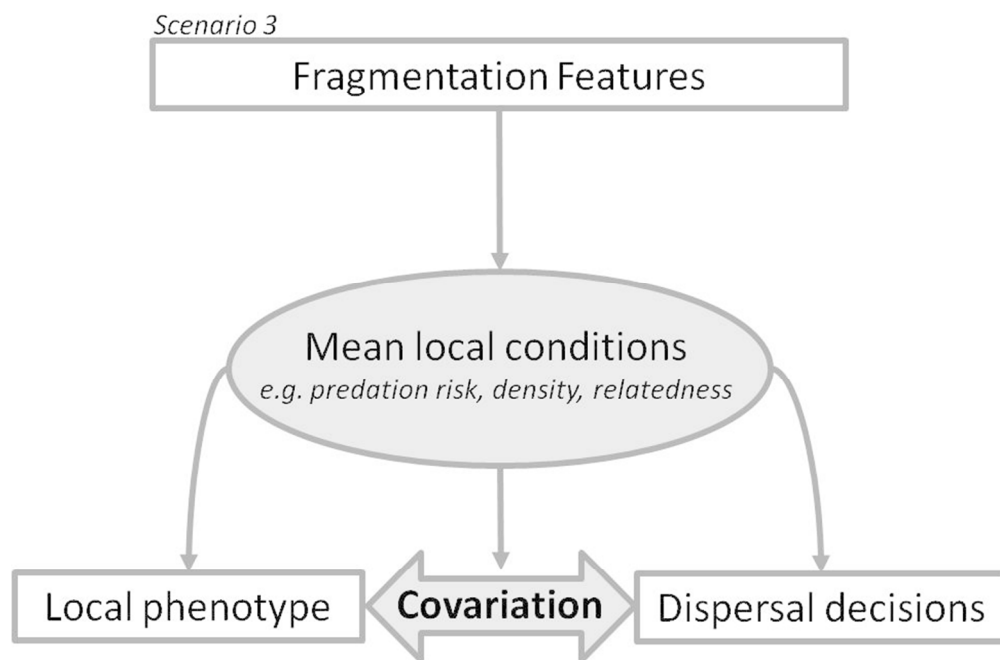
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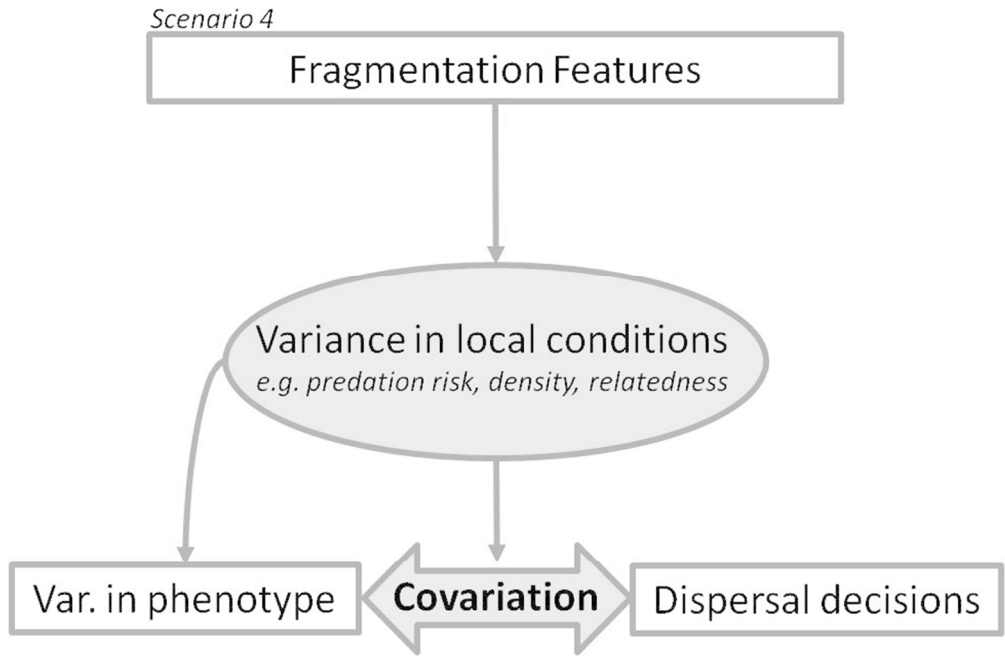
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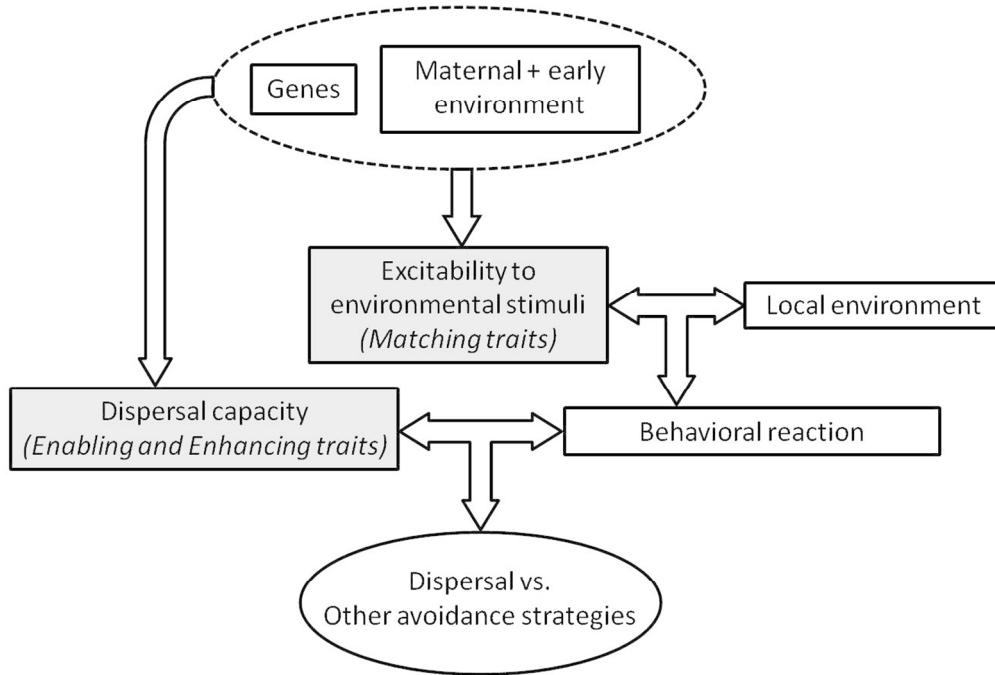
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