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# 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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**Introduction: the multidimensional dispersal process**

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     McPeek 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

98    evidence of non-random dispersal (Edelaar and Bolnick 2012), it is not yet often incorporated

99    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

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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, *Proclossiana 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 (McPeek 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, McPeek 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),

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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 propensies 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 (McPeek 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

18

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.

19

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, McPeek 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.

545      2015) acting on dispersal capacity and propensity. We suggest that individual variation in

546      sensitivities may be important and that dispersal can be a behavioral response to

547      'excitabilities' (i.e. sensitivities) to different environmental stimuli (Fig. 2). A suite of

548      *matching traits*, genetically and environmentally determined, could underlie individuals'

549      excitability to environmental conditions and whether individuals would react "negatively" to

550      local conditions or not. An individual would disperse away from local conditions rather than

551      opt for another stressors avoidance strategy (e.g. hiding in a predator context, submissive

552      behavior in a competition context, Dantzer 1989, Koolhaas et al. 1999) depending on its

553      dispersal capacity. This dispersal capacity would result from a suite of *enabling* and

554      *enhancing traits*. This framework differentiates two categories of phenotype-dispersal

555      associations.

556      The first compiles phenotypic traits (i.e. *enabling* and *enhancing traits*) that are linked

557      to dispersal capacity (e.g. locomotor skills). Such covariations with dispersal behavior (i)

558      would vary in strength, not in direction (e.g. dispersers have similar or better, but not worse,

559      locomotor skills than residents); (ii) would have a significant genetic determinism and; (iii)

560      would have a strong potential to evolve in a fragmented landscape towards a polymorphism of

561      dispersal strategies. These phenotypic specializations would therefore be carried by most

562      dispersers.

563      The second category groups together phenotypic traits (i.e. *matching traits*) that

564      appear genetically uncoupled from dispersal. These traits (i) can covary positively, negatively

565      or not with dispersal behavior depending on local conditions. Their covariations with

566      dispersal behavior are (ii) less likely genetically determined and; (iii) in a fragmented

567      landscape, should reflect the evolution of conditional dispersal. Excitability to certain

568      environmental conditions, leading to emigration or other risk avoidance behavior, could

569      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

27

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

**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    covariatons 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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**Figure legend**

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

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

46

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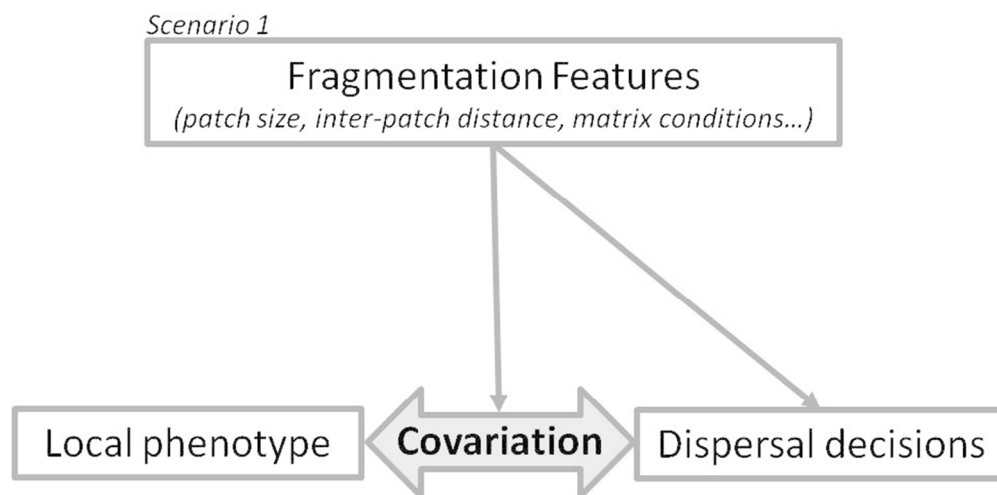**Table 1: Predicted effects of fragmentation on dispersal decision, on phenotypic traits and on their covariances (i.e. dispersal syndromes)**

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

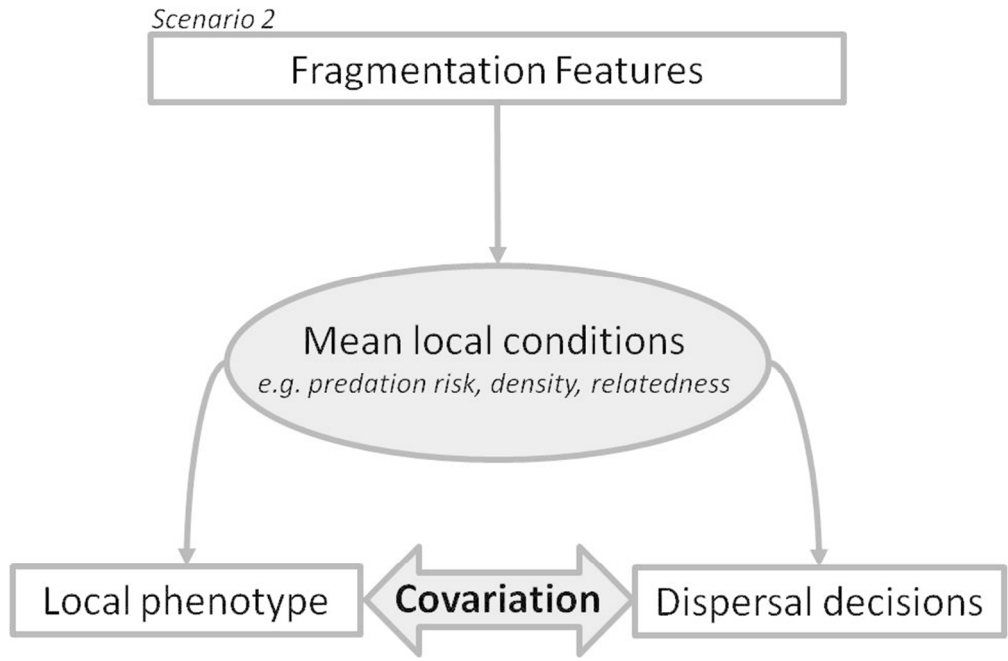| | Environmental condition[a] | Dispersal traits changed[b] | Potential traits changed[c] | Whose phenotype changed?[d] Are covariances changed? | Scenario (Fig. 1)[e] |
|---|---|---|---|---|---|
| **Local conditions** | Predation risk (+) | Emigration prob. (+)[28,29,36,37,40,89] Distance moved (+)[38,40]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

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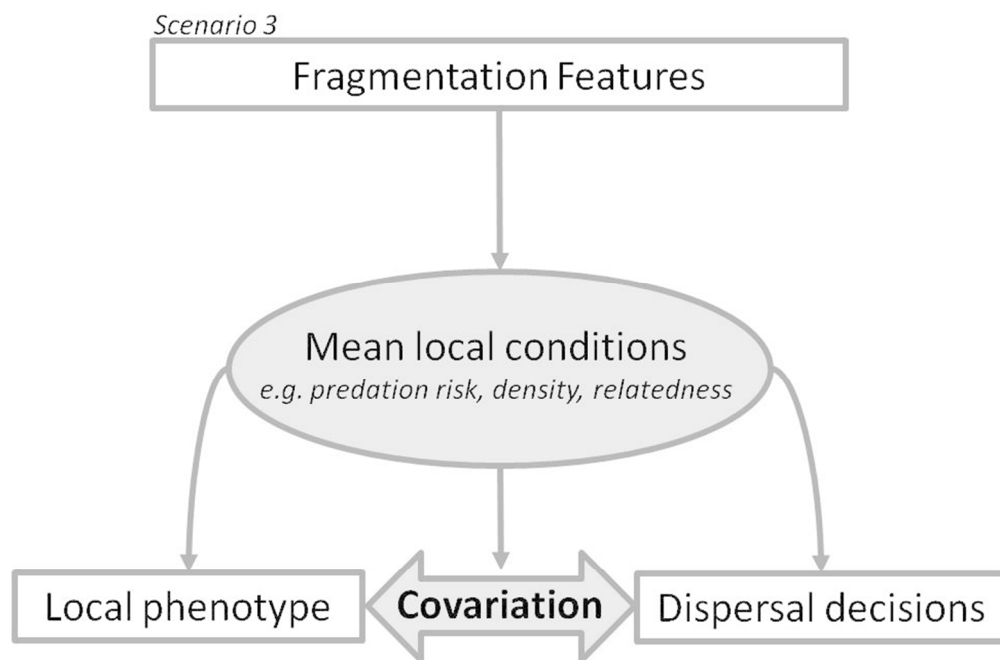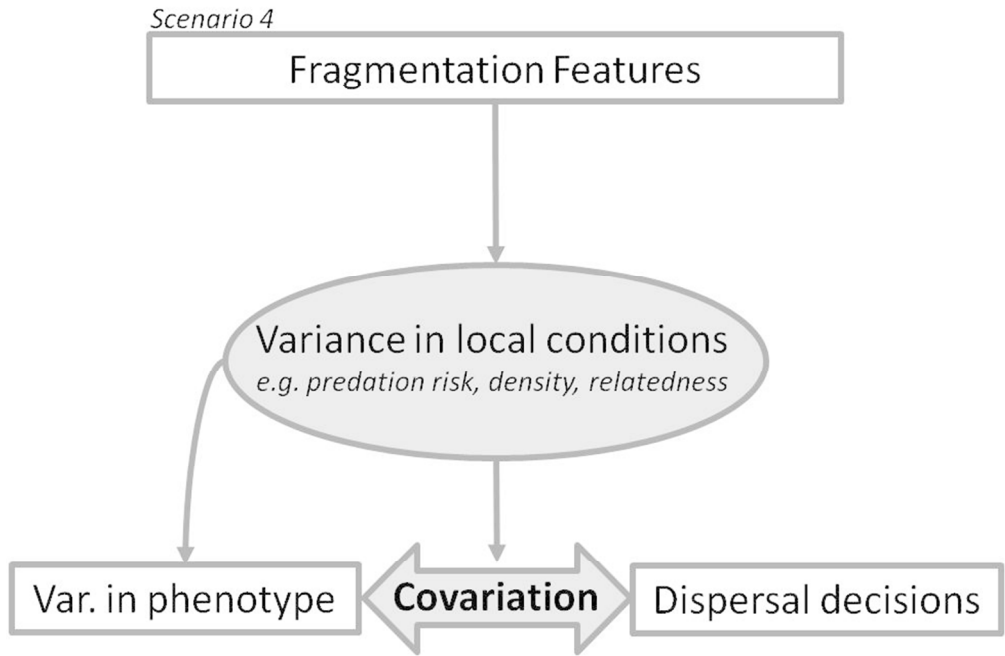
*Scenario 1*

Fragmentation Features
*(patch size, inter-patch distance, matrix conditions...)*

Local phenotype ⇐ **Covariation** ⇒ Dispersal decisions

164x82mm (150 x 150 DPI)

164x109mm (150 x 150 DPI)

164x109mm (150 x 150 DPI)

*Scenario 4*

Fragmentation Features

Variance in local conditions
*e.g. predation risk, density, relatedness*

Var. in phenotype ⟨ **Covariation** ⟩ Dispersal decisions

165x109mm (150 x 150 DPI)

221x149mm (150 x 150 DPI)