

1 **Title:** Evolution of dispersal and the maintenance of fragmented metapopulations

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9

10 **ABSTRACT:**

11

12 Because it affects dispersal risk and modifies competition levels, habitat fragmentation directly
13 constrains dispersal evolution. When dispersal is traded-off against competitive ability,
14 increased fragmentation is often expected to select higher dispersal. Such evolutionary effects
15 could favor the maintenance of the metapopulation by fostering spatial rescue effects. Using an
16 evolutionary model, we first investigate how dispersal evolves in a metapopulation when
17 fragmentation and aggregation of this fragmentation are fixed. Our results suggest that high
18 fragmentation indeed selects for dispersal increase, but this effect is largely reduced in
19 aggregated landscapes, to the point of being nonexistent at the highest aggregation levels.
20 Contrasted dispersal strategies coexist at high fragmentation levels and with no or low
21 aggregation. We then simulate time-varying fragmentation scenarios to investigate the
22 conditions under which evolutionary rescue of the metapopulation happens. Faster evolution of
23 dispersal favors the persistence of the metapopulation, but this effect is very reduced in
24 aggregated landscapes. Overall, our results highlight how the speed of evolution of dispersal

25 and the structuration of the fragmentation will largely constrain metapopulation survival in
26 changing environments.

27

28 **Keywords:** Dispersal evolution, fragmentation, metapopulation, evolutionary rescue, spatial
29 autocorrelation

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31

32 INTRODUCTION

33 Dispersal, defined as the movement of individuals associated with gene flows across
34 space (Ronce, 2007), is a key process in ecology and evolution. It has important consequences
35 for population dynamics, changes in species distribution, maintenance of genetic diversity and
36 for local adaptation (Travis et al., 2013). Habitat loss and fragmentation result in decreased
37 population sizes and gene flows, which undermines population viability and ultimately species
38 survival. In landscapes that include suitable and unfavorable patches of varied size and
39 distribution, dispersal allows individuals to move between suitable patches thereby favoring the
40 survival of the metapopulation through spatial rescue effects (Levins, 1969). In a source-sink
41 context, dispersal increases spatial occupancy as source populations allow the persistence of
42 peripheral sink populations through dispersal (Pulliam, 1988). The maintenance of sink
43 populations is especially important in the context of current changes as source-sink hierarchies
44 could change in time. Given such environmental changes, dispersal helps the survival of species
45 by allowing them to follow suitable niche conditions, thereby playing a key role in range
46 expansions (Phillips et al., 2006).

47 Habitat fragmentation creates spatial heterogeneities in several ways. It decreases the
48 quantity of suitable habitat by decreasing the size and increasing the isolation of suitable
49 patches, even though it increases their number (Fahrig, 2003). In our study, fragmentation is
50 defined by the proportion of hostile vs. suitable locations (patches) and we systematically vary
51 its degree of spatial aggregation. Dispersal evolution is affected by fragmentation, due to
52 variations of different selective pressures. By definition, fragmentation increases spatial
53 heterogeneity so that dispersing propagules encounter non-suitable patches more frequently.
54 Theoretical and empirical studies suggest that such increases in dispersal costs and in spatial
55 heterogeneity select decreased dispersal (Bonte et al., 2006; Cheptou et al., 2008; Duputié &
56 Massol, 2013; Hastings, 1983; Schtickzelle et al., 2006; Travis & Dytham, 1999). While such

57 a counterselection of dispersal was originally highlighted in theoretical models (Hastings, 1983;
58 Travis & Dytham, 1999), empirical evidence for such effects has accumulated in recent years,
59 for a large variety of species, from the weed *Crepis sancta* (Cheptou et al., 2008), to the
60 butterfly *Proclossiana eunomia* (Schtickzelle et al., 2006) and the wolf spider *Pardosa*
61 *monticola* (Bonte et al., 2006). Habitat fragmentation however also increases inbreeding, kin
62 competition or temporal variation of the environment and all of these components usually select
63 for higher dispersal abilities (Charlesworth & Charlesworth, 1987; Cote et al., 2017; Duputié
64 & Massol, 2013; Gandon, 1999; Hamilton & May, 1977; Matthysen et al., 1995; Oldfather et
65 al., 2021; Tung et al., 2018). In addition to the modulation of overall dispersal levels,
66 fragmentation can also, under certain conditions, maintain contrasted dispersal strategies
67 simultaneously. Previous investigations suggest that such a dispersal polymorphism evolves
68 under high fragmentation and high aggregation, with dispersing and non-dispersing individuals
69 coexisting within the same population (Bonte et al., 2010). It principally appears because
70 aggregation produces a coexistence of many small patches and few large patches (Massol et al.,
71 2011; Parvinen, 2002; Parvinen et al., 2020), or due to edge effects that select low dispersers at
72 the edge and high dispersers in central places (Travis & Dytham, 1999).

73 While these previous studies consider dispersal as an isolated trait, it is now widely
74 recognized that evolutionary changes in dispersal most often imply variations in phenotypic
75 traits that constrain other ecological interactions (Raffard et al., 2022). It has been highlighted
76 that when colonization abilities (here our measure of dispersal) are traded against competitive
77 abilities, coexistence of a large number of strategies is possible along this hierarchy (Tilman,
78 1994). This trade-off has a long history in ecology and former studies investigated how it may
79 explain the coexistence of species within metacommunities (Calcagno et al., 2006; Tilman et
80 al., 1997; Yu & Wilson, 2001) and how such a diversity varies when fragmentation or habitat
81 destruction occurs (Tilman et al., 1994, 1997). While these studies mostly focused on ecological

82 dynamics, we here use the trade-off to investigate its eco-evolutionary implications in a
83 fragmentation context. Such a trade-off could for instance occur because given a fixed quantity
84 of energy, allocation could produce a large number of small propagules (colonizer) or few large
85 propagules (competitor) (eg, Geritz et al., 1999; Smith & Fretwell, 1974). For example, the
86 weed *Crepis sancta* produces small and/or large seeds. Small seeds have high wind dispersal
87 due to their lightweight but low competitiveness due to low resource storage. In contrast, large
88 seeds have restricted dispersal due to their weight but contain more resources (Cheptou et al.,
89 2008). In social insects, dispersal and reproduction could follow from the production of many
90 isolated queens that fly large distances and have high mortality or through the split of the colony
91 in a few propagules that usually disperse on short distances but may be more efficient at
92 gathering resources when founding the new colonies (Cronin et al., 2013, 2016). Habitat
93 fragmentation affects strategies along the competition-colonization trade-off in different ways.
94 First, it directly lowers the average density at the metapopulation level, thereby changing
95 competitive pressures. Second, it creates isolated patches that act as a positive filter for the best
96 dispersers. To our knowledge, only one study considers how this competition/colonization
97 trade-off affects the dispersal strategies selected by fragmentation (Tilman et al., 1994). This
98 study shows that in a spatially variable environment with an increase of fragmentation, the more
99 competitive (and thus the less dispersive) strategies disappear first, so that high dispersal
100 strategies are selected.

101 Such results are obtained without considering explicit spatial structures as the position
102 of patches is not accounted for in Tilman et al. (1994) (mean field approximation).
103 Fragmentation of the environment can however be an aggregated process, as human activities
104 such as urban development or agricultural exploitation are often concentrated in specific
105 locations. A previous work on metapopulations shows that the structuration of habitat
106 heterogeneities is crucial to study metapopulation responses to fragmentation (Hiebeler, 2000).

107 When environmental heterogeneities are spatially correlated (aggregation), predictions based
108 on mean-field approximation are often qualitatively incorrect when compared to spatially
109 explicit approaches (Hiebeler, 2000). In contrast, mean-field approximations yield correct
110 results in the case of randomly distributed fragmentation. Leaving out the
111 competition/colonization trade-off, the importance of aggregation in the evolution of dispersal
112 is highlighted by various studies (Bonte et al., 2010; Fronhofer et al., 2014; Ovaskainen et al.,
113 2002; Travis & Dytham, 1999). For example, in the context of correlated extinctions, empirical
114 work on the spider mite *Tetranychus urticae* and an associated theoretical model show a
115 selection for long-distance dispersal and a decrease of local dispersal compared to spatially
116 random extinctions (Fronhofer et al., 2014). Travis and Dytham (1999) found a decrease in
117 dispersal with increased fragmentation, but an increase in dispersal with higher aggregation.
118 The risk to disperse outside of a large aggregate of suitable patches and into a hostile
119 environment is indeed lowered, so that aggregation modulates dispersal costs. Similarly, Bonte
120 et al. (2010) found a decrease of local and global dispersals with the increase of fragmentation,
121 and demonstrates that decreasing aggregation has the contrasted effect of decreasing local
122 dispersal and increasing global dispersal. To summarize, the study that considers variations of
123 dispersal strategies along a competition/colonization trade-off in fragmented habitats use a
124 spatially implicit (mean field) approach, while others use spatially explicit landscapes but
125 ignore possible competition/colonization trade-offs. The goal of our study is therefore to
126 integrate both aspects, that is to study the evolution of dispersal along the
127 competition/colonization trade-off given a spatially explicit structuration of the habitat.

128 Understanding this dispersal evolution has immediate consequences to better predict the
129 maintenance of metapopulations. For instance, a selected increase in dispersal favors the
130 exchange of individuals between patches and the colonization of empty patches (spatial rescue).
131 Extinction may also be prevented, by the emergence of evolutionary rescue, when natural

132 selection favors adapted traits (Bell, 2017; Carlson et al., 2014; Gomulkiewicz & Holt, 1995).
133 Here, an evolutionary increase of dispersal distances could avoid a population extinction in a
134 climate change context (Boeye et al., 2012) or in a context of high mortality (Heino & Hanski,
135 2001). Given a temporally increasing fragmentation, natural selection may favor high dispersal,
136 as the availability of empty and isolated patches constantly increases. Because only highly
137 dispersive strategies can reach them, such isolated patches act as filters that favor high dispersal
138 (Heino and Hanski, 2001). Consistent with this theoretical prediction, a temporal increase of
139 fragmentation led to higher dispersal in *Drosophila melanogaster* experiments (Tung et al.,
140 2018). Conversely, if evolution were to lead to less dispersal, it would potentially decrease
141 metapopulation persistence (Gyllenberg et al., 2002). The implication of the evolution of
142 dispersal for metapopulation persistence in a world that becomes increasingly fragmented is
143 therefore an important, unresolved issue.

144 Using metapopulation simulations, we studied how the spatio-temporal structuration of
145 fragmented environments acts on dispersal evolution given a competition/colonization trade-
146 off. First, we fixed fragmentation and aggregation levels and investigated how dispersal
147 evolved. Second, we varied fragmentation over time to test whether dispersal evolution can
148 prevent extinction (evolutionary rescue), under various rates of evolution of dispersal. We
149 hypothesize that, in a fixed environment, higher fragmentation selects for an increase in
150 dispersal because more empty patches will become available to colonizers and inaccessible to
151 competitors. In addition, competition could be relaxed in fragmented landscapes as the average
152 occupancy is lowered. However, if the fragmentation is aggregated, large groups of suitable
153 patches could persist in the landscape. Such a situation is favorable to competitors and should
154 decrease the selection toward higher dispersal or lead to dispersal polymorphism with
155 competitors dominating aggregated patches while colonizers remain favored in isolated
156 patches. When fragmentation increases over time, we hypothesize that the occurrence of

157 evolutionary rescue depends on the speed of evolution of dispersal, which needs to be faster
158 than the speed of fragmentation to counterbalance its effects.

159

160 **MODEL PRESENTATION**

161 Simulations and analysis were done with R 3.9. Our simulations consider a spatially
162 explicit environment consisting of a grid of 50x50 patches wrapped into a torus to avoid edge
163 effects (Fig. 1). Each patch can be in one of three possible states: unsuitable, suitable and empty
164 or suitable and occupied. Only suitable and empty patches are available to dispersing
165 individuals. Importantly, we define fragmentation as the percentage of unsuitable patches. This
166 definition of fragmentation is classically considered in the literature and is directly linked to
167 other components often used to describe fragmentation such as the number of independent
168 patches, their size or their isolation (Fahrig, 2003). For a given level of fragmentation, we
169 independently vary the degree of aggregation of unsuitable patches, as controlled by the Hurst
170 coefficient. This coefficient is directly related to how similarity among patches decrease with
171 distance thereby constraining spatial autocorrelation. While we keep a simple definition of
172 fragmentation (proportion of unsuitable patches), note (1) that higher frequency of unsuitable
173 patches decreases overall connectivity; (2) that we also manipulate the effect of fragmentation
174 on local contexts by considering varying degrees of aggregation. Examples of landscapes can
175 be found in the upper left part of Fig. 1. Unsuitable patches are distributed randomly or with a
176 set percentage of aggregation (created with a fractal Brownian motion) using the *NLMR* and
177 *landscapetools* package (Sciaini et al., 2018). A higher aggregation means that a suitable patch
178 is more likely to be close to another one compared to the random expectation.

179 Individuals are characterized by two traits: colonization and competition capacities
180 (both integer values) directly linked through the colonization/competition trade-off. The model

181 relies on discrete time steps, each time step being divided in three parts: colonization,
182 competition and extinction (see Fig. 1).

183 (1) Colonization. The colonization capacity defines the radius (number of patches) of the
184 area around the individual where its offspring are dispersed. We assume that offspring
185 will potentially colonize all empty but suitable patches within this range. This implicitly
186 assumes that individuals with larger colonization capacity are not limited by the number
187 of offspring they produce, assuming an increase of fecundity when dispersal distance
188 increases (see introduction).

189 (2) Competition. We assume that only empty suitable patches can be colonized by
190 propagules. Given that individuals fill all suitable surrounding patches with their
191 offspring, suitable empty patches are often reached by several offspring simultaneously.
192 We then assume that the competitive hierarchy favors the strategy that has the smallest
193 dispersal distance (competition-colonization trade-off, lower part of Fig. 1). The
194 surviving individual inherits the dispersal strategy of its parents, except in the case of
195 rare mutation events. When mutation occurs, the dispersal range of the mutant
196 individual is enhanced or reduced by one cell, with equal probability. Mutations incur
197 incremental variations in dispersal distance of 1, upward or downward, with equal
198 probability. Dispersal distances below 0 are not possible and discarded. Note that while
199 this situation is never observed here, a dispersal distance above 25 would mean global
200 dispersal over the whole grid. We assume that established individuals (ie, occupied
201 patches) cannot be displaced by incoming propagules, regardless of their traits.

202 (3) Extinction. We assume that extinction probability does not depend on the dispersal trait.
203 Occupied suitable patches therefore become empty (but still suitable) with a fixed
204 probability e at each time step ($e=0.05$).

205 Each landscape is populated, at the beginning of the simulation, with ten populations
206 that are randomly distributed on suitable patches. These populations are assumed to be highly
207 dispersive (colonization capacity of twelve). We verified that initial conditions (number of
208 populations and initial colonization capacity) do not affect the equilibrium outcome
209 (Supplementary information Figure 1).

210

211 *Scenario 1: Evolution of dispersal in fixed fragmented landscapes*

212 In the first scenario, we fix the landscape and study how dispersal evolution depends on
213 the levels of fragmentation and aggregation. Fragmentation corresponds to a specified
214 percentage of unsuitable patches (i.e. 0, 20, 40, 60, 80, 90, 95 or 99% of patches are assumed
215 unsuitable). These unsuitable patches are aggregated at varying degrees (0, 20, 40, 60, or 80%).
216 To assess repeatability, twenty different landscapes are generated for each combination of
217 fragmentation and aggregation. The mutation rate is set at 0.1. Each simulation lasts 50 000-
218 time steps. Because simulations are stochastic, they never reach a completely stable
219 equilibrium, but we visually checked for each simulation that 50 000 time steps allowed the
220 system to reach a stable regime that can be characterized (Figure S2). It means that the mean
221 and the variance stay stable over at least 5 000 time steps (more discussion is provided in
222 supplementary information S2). We record the mean dispersal capacities of individuals during
223 the simulation and the occupancy of each dispersal strategy.

224

225 *Scenario 2: Evolutionary rescue under progressively increasing fragmentation*

226 In the second scenario, we progressively increase the level of fragmentation over time.
227 We systematically manipulate the rates of fragmentation and of mutation to investigate
228 conditions under which dispersal evolution can delay extinction. The grid is supposed to be
229 fully suitable at the onset of the simulation and for the first 200-time steps. We then

230 progressively increase fragmentation until the metapopulation becomes extinct. As in the first
231 scenario, the increase in fragmentation occurs with random or aggregated distributions of
232 unsuitable patches (levels of aggregation: 0%, 10%, 20%, 40%, 60%, 80%). Rates of
233 fragmentation correspond to the probability that a suitable patch becomes unsuitable within a
234 given time step. We tested three rates of fragmentation (0.0001, 0.001, 0.01). As evolutionary
235 rescue is construed as a race between the speed of the disturbance and the speed of adaptation
236 (Gomulkiewicz & Holt, 1995), we also systematically manipulate the speed of evolution by
237 considering different rates of mutation (0.001, 0.01, 0.1). We replicate each combination of
238 aggregation, fragmentation rate and mutation rate forty times. We record the fragmentation at
239 population extinction as an index of the resistance of the metapopulation to the disturbance.
240 Higher values of this index show that evolution of dispersal allowed the metapopulation to
241 survive higher levels of the disturbance. Evolutionary rescue occurs if metapopulations with
242 evolution of dispersal resist higher disturbance levels than metapopulations without dispersal
243 evolution. For each set of simulations, we also record the variations of dispersal strategies
244 (occupancy of the various dispersal phenotypes) over time to identify the path that evolutionary
245 rescue takes.

246

247 **RESULTS**

248 *Evolution of dispersal in fixed fragmented landscapes*

249 Higher fragmentation selects for increasing mean dispersal distances. In non-
250 fragmented landscapes, competitive strategies eventually dominate so that dispersal distance
251 quickly evolves close to one (Fig. 2a and b). Such a strategy remains dominant for all low levels
252 of fragmentation (0 to 60%). High dispersal is selected under higher fragmentation, especially
253 strongly when fragmentation is random (7.27 ± 1.08 patches at 99%, red line in Fig. 2a, see also

254 Fig. 2c). However, adding aggregation strongly decreases this selection effect. For instance, a
255 little bit of aggregation (20%, orange line in Fig. 2a, see also Fig. 2d) suffices to lower the
256 selected dispersal distance in very fragmented landscapes to 2.09 ± 1.02 patches. Higher
257 aggregation (40 to 80%) further decreases the selected dispersal distance, so that fragmentation
258 hardly has any effect on selected dispersal when aggregation is high (blue lines, Fig. 2a).
259 Aggregation therefore qualitatively changes the results of mean field models (such as Tilman
260 et al., 1994).

261 *Evolution of polymorphism in fragmented landscapes.*

262 Beyond the observed variations in mean dispersal distances, the long-term variability of
263 dispersal strategies also depends on fragmentation and aggregation. Particularly, when
264 fragmentation is sufficient, we observe the coexistence of several dispersal strategies
265 (polymorphism, Fig. 3). In all cases of polymorphisms, we observe similar patterns. Suitable
266 patches that are close to one another sustain the less dispersive strategies, while isolated patches
267 act as filters that favor the more dispersive strategies. The set of polymorphic strategies however
268 vary depending on the relative positions of patches. For instance, given a very high
269 fragmentation (99%) with no or little aggregation (20% or less), few suitable patches are close
270 to one another by chance (purple patches, Fig. 3b). Because the distances among these patches
271 is still quite important, the dispersal strategy they sustain is still quite high (around 5). Other
272 patches are more isolated (blue patches, Fig. 3c) and act as a selective pressure favoring very
273 high dispersal distances (around 9). When fragmentation is slightly lower (80 to 95%) and
274 aggregation slightly higher (20 to 40%), large aggregates of suitable patches occur in the
275 landscape (red patches, Fig. 3e) and favor competitive strategies (dispersal distance around 1).
276 The remaining suitable patches are isolated and favor a continuum of more dispersive strategies.

277 *Evolutionary rescue under progressively increasing fragmentation*

278 When fragmentation increases over time, fast dispersal evolution allows a longer
279 persistence of the metapopulation, i.e. an evolutionary rescue. Fig. 4 shows this evolutionary
280 rescue as the difference (orange arrows) between the scenario with no evolution (mutation rate
281 equal zero) and the three scenarios with more or less rapid evolution. Intuitively, evolutionary
282 rescue occurs and is strongest when there is no aggregation, fragmentation rate is low, and
283 mutation rate is high (mean difference of 3.04% between scenarios without and with evolution,
284 Fig. 4a). Evolutionary rescue is largely decreased when fragmentation rate is higher (a
285 difference of 0.63%, Fig. 4c). Variations in the potential of evolutionary rescue are not
286 continuous. Rather, a jump in the extinction time when mutation rates increase can be identified.
287 This jump is relative to the fragmentation rate. Under our set of parameter values, evolutionary
288 rescue occurs when the mutation rate is ten times higher than the fragmentation rate (Fig. 4a,b,c,
289 blue arrows). Finally, we stress that aggregation largely constrains evolutionary rescue. No
290 potential for evolutionary rescue can be identified in aggregated landscapes (Fig. 4d,e,f).

291

292 **DISCUSSION**

293 Our study shows an increase of dispersal capacities in fragmented landscapes in the
294 context of competition/colonization trade-offs. Aggregation acts as an opposite force, as
295 decreased dispersal is selected in more aggregated landscapes. At high fragmentation and low
296 aggregation, different strategies can be selected and can coexist, with better competitors in
297 aggregated patches and better colonizers in isolated patches. Such an evolution of
298 polymorphism allows a good global coverage of available space. When fragmentation increases
299 with time, the rapid evolution of dispersal facilitates the survival of the metapopulation but this
300 evolutionary rescue effect can only be observed in non-aggregated landscapes and when
301 fragmentation rate is not too high.

302 The selection of more dispersive strategies in fragmented landscapes in a context of
303 competition/colonization trade-offs is congruent with Tilman et al. (1994) which also relies on
304 this trade-off. Other studies on the evolution of dispersal in spatially heterogeneous systems,
305 but in the absence of a competition/colonization trade-off, show a reverse pattern, as dispersal
306 is then counter selected because dispersal costs are enhanced by spatial heterogeneities
307 (Hastings, 1983; Travis & Dytham, 1999). This highlights that patterns of selection strongly
308 depend on the trade-off structure associated with dispersal traits. Recent works highlight the
309 importance of dispersal syndromes (Raffard et al., 2022; Stevens et al., 2014), i.e. the fact that
310 dispersal traits may be directly coupled to traits defining ecological interactions. The
311 competition/colonization trade-off falls within this category, as variations of dispersal are
312 directly coupled to competition hierarchies. Our results therefore highlight how such a
313 syndrome could lead, for some landscapes, to the selection of higher dispersal, while works that
314 consider evolution of dispersal alone (eg, Hastings, 1983; Travis and Dytham, 1999) would
315 produce the reverse pattern. Application of either framework of course depends on the types of
316 organisms that are considered and whether dispersal traits are competitively costly.

317 In particular, our model assumes that the fecundity of the organism under consideration,
318 i.e. the number of offspring produced, increases with increasing dispersal distance. This
319 provides an additional advantage for dispersive strategies that will produce many more
320 offspring and therefore occupy space more quickly if there is no superior competitor present.
321 Many previous models do not make this assumption and use constant fecundity (eg, Bonte et
322 al., 2010; Travis and Dytham, 1999). This hypothesis may influence our results in several ways.
323 With constant fecundity, selection of dispersive strategies is likely reduced, leading to a smaller
324 mean dispersal in highly fragmented habitats, lower abundances in the landscape, and early
325 extinctions. Dispersal polymorphism should stay present because isolated patches can only be
326 reached by dispersive strategies. However, this assumption of increasing fecundity with

327 increasing dispersal distance is not biologically irrelevant and can be linked to various groups
328 of organisms. A certain amount of energy could be allocated in either a few large, poorly
329 dispersing offspring or in many small, highly dispersing offspring. This rationale has been
330 largely used in the context of variations of plant seed size (eg, Henery & Westoby, 2001;
331 Muller-Landau et al., 2008). It could also apply in the context of social insect colonies. For
332 instance, in ants with the production of large propagules consisting of a queen and workers that
333 disperse over short distances or small propagules of a single queens dispersing over long
334 distances (Cronin et al., 2013).

335 We explain the selection of higher dispersal in fragmented landscapes by two
336 mechanisms. First, fragmentation decreases overall occupancy (on the entire grid). Thereby,
337 when a patch is emptied, the number of possible colonizers (ie, of suitable filled patches) is
338 reduced. This reduces the average competition level. The advantage of competitive strategies
339 is therefore reduced. Second, fragmentation intensifies the strength of the competition for space
340 which favors colonizers. Isolated patches in fragmented landscapes can only be exploited by
341 highly dispersive strategies. Effects of fragmentation on mean levels of dispersal have led to
342 contrasted results in empirical studies (Cheptou et al., 2017). Our results of a selection of higher
343 dispersal is for instance coherent with empirical studies of nuthatches (*Sitta europaea*) in
344 Belgium (Matthysen et al., 1995). Similarly, metapopulation study of the Glanville fritillary in
345 Finland shows that isolated patches of the metapopulation act as positive filters for the more
346 dispersive strategies (Hanski et al., 2004) and that this variation can be linked to allelic
347 variations constraining flight metabolism (Haag et al., 2005). Conversely, a decrease of
348 dispersal at higher fragmentation levels has been observed in various animal or plant species
349 (Bonte et al., 2006; Cheptou et al., 2008; Schtickzelle et al., 2006). Spatial heterogeneity and
350 competition decrease are two forces that act with opposite effects, the former decreasing
351 dispersal (higher dispersal cost) while the latter increases it (decreased abundancies in

352 fragmented landscapes, relax competition). The importance of each force varies among species
353 and needs to be systematically considered to better predict changes in dispersal.

354 We found that aggregation largely reduces the selection of dispersal strategies, to the
355 extent that such a selection cannot even be detected when aggregation is larger than 40%. This
356 points out the importance of spatially explicit models. In a previous work, Hiebeler (2000)
357 showed how mean field approximations provide accurate occupancy predictions for random
358 fragmented landscapes, but not when aggregation exists. Similarly, we show here that while
359 our results on dispersal evolution in random landscapes are coherent with mean field
360 approximations (Tilman et al., 1994), such approximations do not provide qualitatively
361 adequate variations when aggregation takes place. We explain the reduction of dispersal due to
362 aggregation by the fact that it favors the replacement of colonizers by competitors because of a
363 high probability to find a favorable patch next to another favorable patch. The landscape is there
364 continuous, so that competition is selected in such localities. Such a result is in line with Bonte
365 et al. (2010) who found an increase of local dispersal (our competitive strategy) and a decrease
366 of long-distance dispersal (our colonizer strategy) in aggregated fragmentation scenarios. We
367 therefore completely agree with the necessity of spatially explicit approaches to better
368 understand the dynamics of fragmented metapopulations (Hiebeler, 2000). Here, a simple
369 mean-field approach would yield an overestimation of dispersal evolution and of associated
370 evolutionary rescue effects.

371 Our model is based on mutations and on the selection of certain phenotypes resulting
372 from these mutations. While our results can be largely interpreted from a selection point of
373 view, we explicitly account for stochastic components, both in the mutation process and in the
374 random patch extinction process. This latter source of stochasticity leads to genetic drift in our
375 simulations. Effects of drift are particularly visible for small metapopulation sizes (ie, on the
376 brink of extinction), and indeed we observed broader distributions of phenotypic values in such

377 conditions. To assess the importance of these stochastic components, we undertook 20
378 replications of each parameter combination in scenario one and 40 in scenario two. The
379 consistent qualitative variations of dispersal distances however suggest a large role of selective
380 processes.

381 We observe dispersal polymorphism when fragmentation is high and aggregation low
382 to intermediate. Such landscapes contain a mix of large aggregates of patches and of isolated
383 patches. The strategy favored in the aggregates of patches is more competitive, and the dispersal
384 distance selected there depends on how loose the aggregates are. When aggregation produces
385 continuous aggregates, the most competitive strategies are favored (dispersal distance close to
386 1, Fig. 3f), while when aggregates are looser, selected dispersal distances could be higher (Fig.
387 3f). In all cases, isolated patches favor more dispersive strategies. These results are coherent
388 with previous theoretical studies that show how fragmentation can favor dispersal
389 polymorphism. In particular, some of them showed that polymorphism is prevalent when few
390 large patches (our patch aggregates) co-occur with small patches (our isolated patches) (Bonte
391 et al., 2010; Massol et al., 2011; Parvinen, 2002; Parvinen et al., 2020). A large literature exists
392 on how ecological dynamics of metapopulations under fragmentation leads to changes in
393 persistence and to variations in diversity (Bascompte & Rodriguez, 2001; Bascompte & Solé,
394 1996; Ovaskainen et al., 2002; Solé et al., 2004). Previous works highlight the critical role of
395 patchiness (Bascompte and Rodriguez, 2001) or of extinction thresholds (Bascompte and Solé,
396 1996). Here, our goal is rather to assess how fragmentation affects the evolution of dispersal
397 and its eco-evolutionary consequences for the metapopulation dynamics. Such an evolution
398 may in turn affect persistence (and diversity) when it fosters evolutionary rescue.

399 Evolutionary rescue can be construed as a race between speed of adaptation and of
400 environmental deterioration. Hence, the faster the evolution and the slower the perturbation, the
401 more likely the rescue. We observe that such expectations are met when fragmentation is

402 random (no aggregation). Dispersal evolution delays the extinction of the population when
403 fragmentation rate is low and mutation rate high. Fast selection of good dispersers then occurs.
404 As these are adapted to occupy isolated patches, such strategies foster spatial rescue in the
405 highly fragmented landscapes. Slow evolution would not allow that. At the onset of
406 fragmentation, the grid is continuous, and mostly occupied by competitors. If fragmentation is
407 too fast, there is no time for dispersers to appear and become selected and to fill isolated patches.
408 Interestingly, our study shows that rescue happens as a jump phenomenon, being only possible
409 when mutation rates are higher (10 times higher in our model) than perturbation rates. No
410 evolutionary rescue occurs when fragmentation is aggregated. Aggregation delays extinction
411 by itself even without evolution. Under high fragmentation and aggregation levels, suitable
412 patches make small continuous groups that facilitate the local persistence of competitors. In an
413 aggregated context, dispersal evolution is absent or strongly constrained (blue curves on Fig.
414 2a) so that little evolutionary potential exists. In the absence of such an adaptive potential,
415 evolutionary rescue cannot act. Our results on the possibility of rescue through evolutionary
416 changes of dispersal agree with former theoretical works where fragmentation either stemmed
417 from climatic changes (Boeye et al., 2012) or from heterogeneities in mortality (Heino &
418 Hanski, 2001). While in the actual context of fast environmental changes, it may seem
419 complicated for species to evolve quickly enough (10 times faster than the perturbation), several
420 examples of fast evolution of dispersal in fragmented systems have been reported (reviewed in
421 Cheptou et al., 2017). Whether such evolution are sufficient to affect long term metapopulation
422 persistence is however unknown. The fact that evolutionary rescue does not happen here in
423 aggregated landscapes also has important implications. The current fragmentation of habitats is
424 a complex non-random process that may be frequently auto-correlated in space, therefore
425 producing aggregated structures. For instance, the construction of additional urban areas next
426 to existing urban areas creates aggregated landscapes. Studies from the Tabriz Metropolitan

427 Area (Iran) show that the destruction of suitable habitats surrounding the cities result in the
428 creation of aggregated non-suitable patches (Dadashpoor et al., 2019b, 2019a). Aggregation of
429 fragmentation can also be linked to the displacement and development of agricultural activities.
430 In Beijing City, China, landscape patterns show important and complicated changes in the
431 distribution of urban and agricultural lands. Economic development expands cultivated land
432 and construction into forests and grasslands resulting in aggregated and less diverse landscapes
433 (Li et al., 2017). We propose that when fragmentation happens in such aggregated ways,
434 evolution will likely play a minor role in the maintenance of the metapopulation.

435 Our study highlights the importance of considering dispersal syndromes (here through
436 the competition/colonization trade-off) and the structuration of habitat fragmentation to better
437 understand how dispersal evolves in disturbed landscapes. We acknowledge that our model is
438 quite simple and can only be used to provide baseline scenarios. For instance, fragmentation
439 can create changes not only in competition intensity, but also in other community aspects (eg,
440 presence of mutualists and enemies, see Cheptou et al., 2017). While we simply focus on the
441 colonization-competition trade-off, evolutionary changes can also involve other phenotypic
442 traits. Colonization of empty patches, usually free of conspecifics, could for instance lead to
443 the fast evolution of intrinsic growth rates (Williams et al., 2019). We hope that the results we
444 present here will motivate efforts to better understand the multidimensionality of dispersal
445 evolution and its implications for the future of biodiversity.

446

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449 **DATA AVAIBILITY**

450 Model and analysis scripts are available on github:

451 https://github.com/bfinand/Model_dispersal_evolution

452

453 **CONFLICT OF INTEREST**

454 The authors declare no conflict of interest.

455

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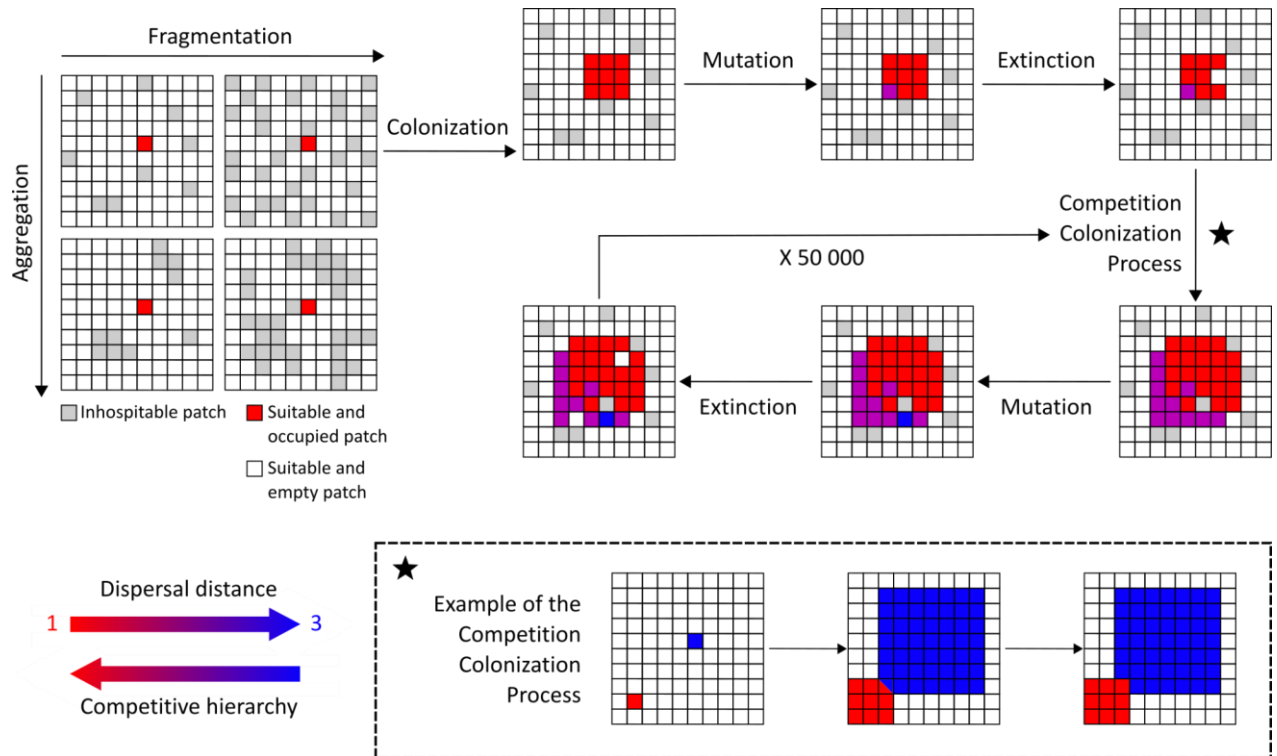
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622 **FIGURES**

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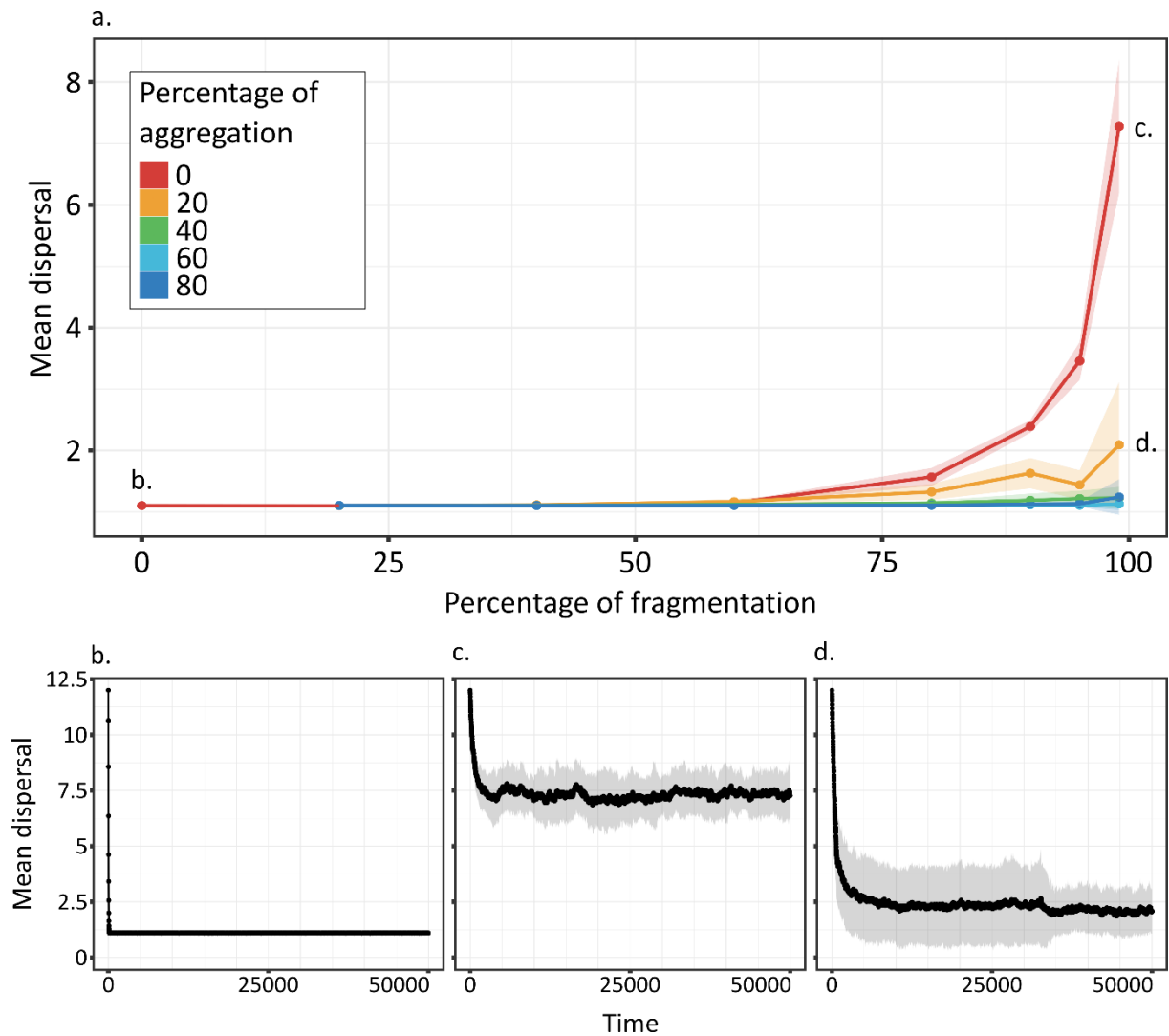
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626 **Figure 1:** Illustration of a simulation based on the competition/colonization tradeoff in a fixed
 627 environment scenario. Upper panels detail the various parts of a given timestep, while the box
 628 below shows the competition/colonization process when two individuals arrive on the same
 629 patch. For each time-step, individuals colonize all suitable and empty patches within their
 630 dispersal distance. Individuals mutate with a small probability. If a mutation occurs, the
 631 dispersal distance of the individual is modified by 1, upward or downward with equal
 632 probability. Extinction events follow, with a probability e . If two (or more) individuals arrive
 633 on the same patch, the one with the smallest dispersal distance, being competitively dominant,
 634 wins the patch. One simulation lasts 50 000 time-steps.

635



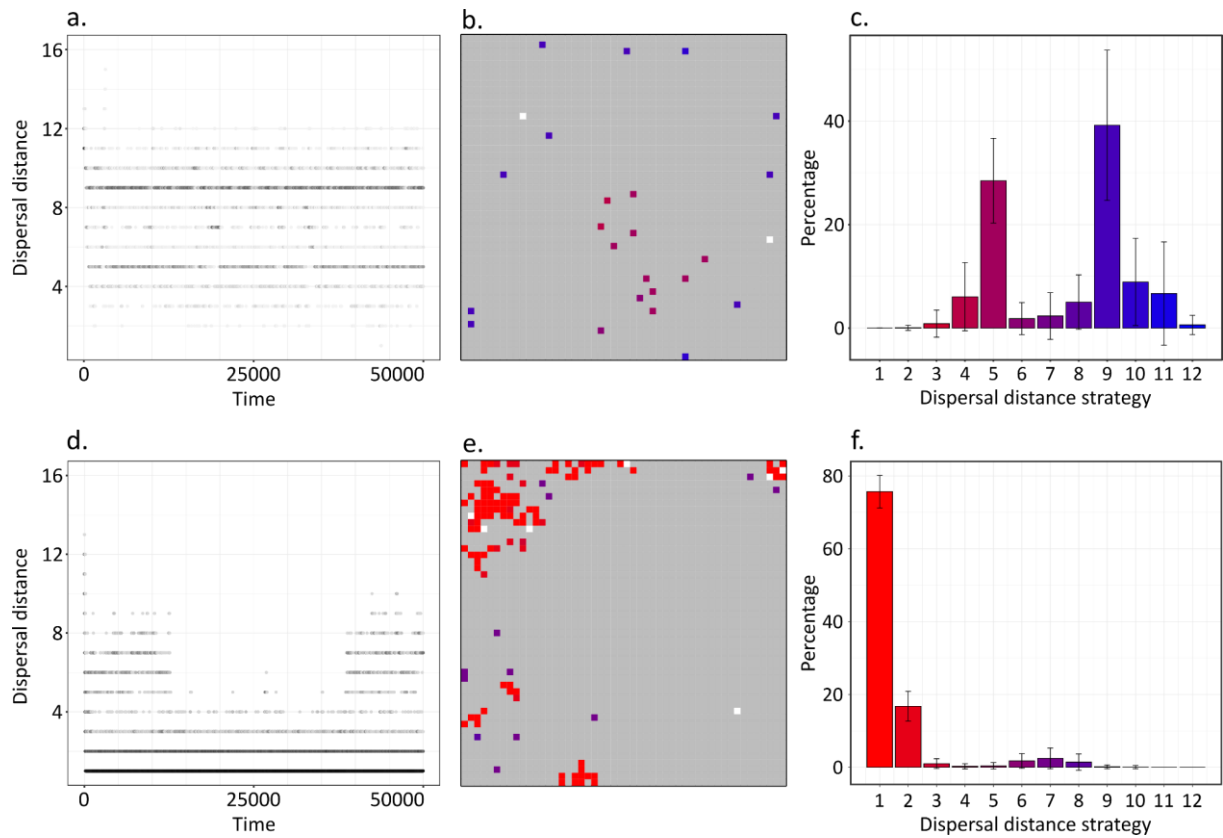
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637 **Figure 2:** Dispersal (mean +/- SD) at the end of simulations (at equilibrium) depending on
 638 environment fragmentation and aggregation (a), and over time (b-d) for the 20 replicates for
 639 conditions of no fragmentation and no aggregation (b), 99% of fragmentation and no aggregation
 640 aggregation (c) or 99% of fragmentation and 20% of aggregation (d). Note that higher dispersal
 641 distance is selected in random fragmented landscapes, but that aggregation of fragmentation
 642 lowers this selective effect. Shadows around curves represent SD.

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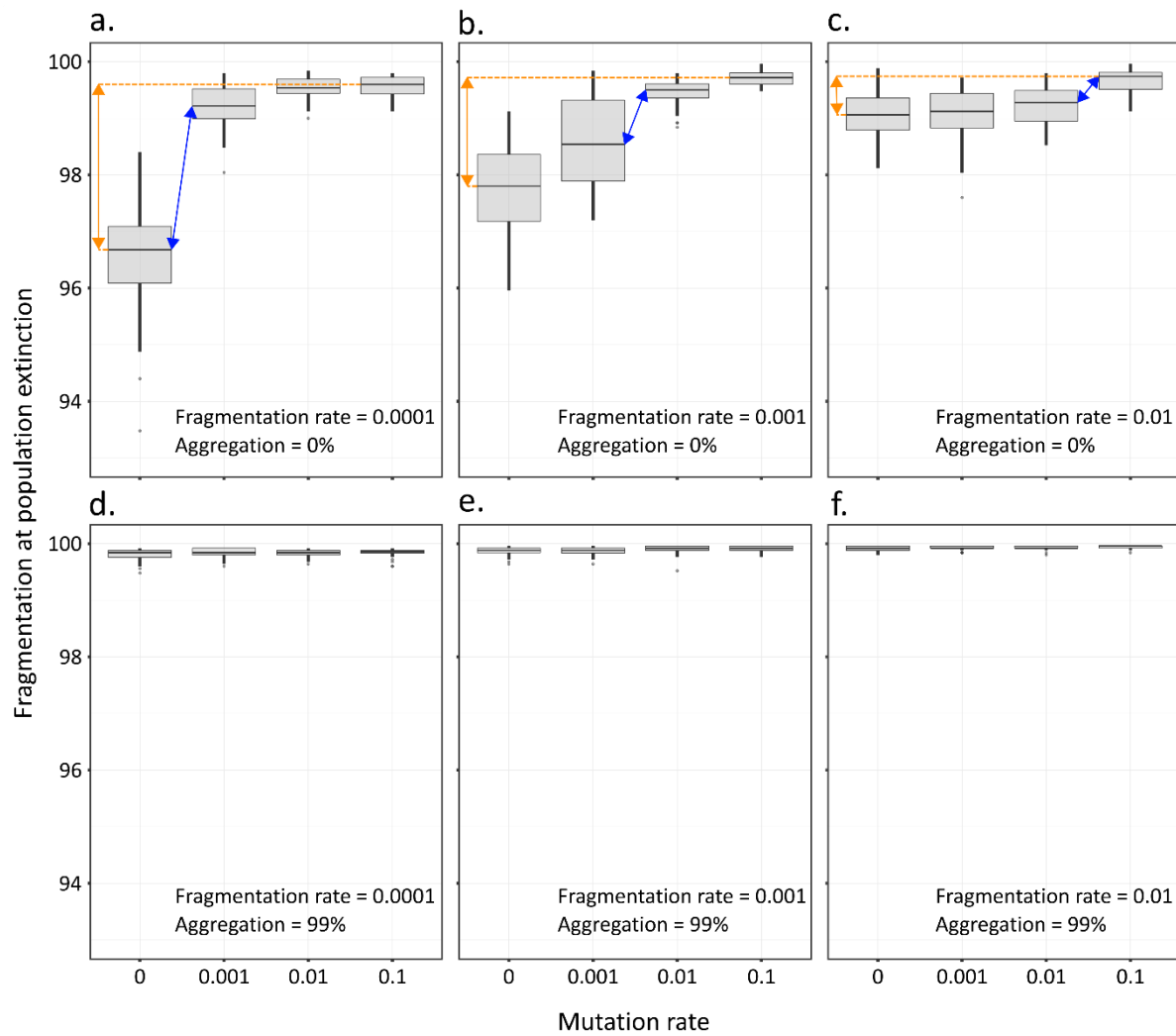
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649 **Figure 3:** 2 examples of simulations showing dispersal polymorphism. (a) and (d) show the
 650 presence of dispersal strategies over time in two separate simulations. (b) and (e) represent the
 651 grid at the end of the corresponding simulations. (c) and (f) show the relative abundance of each
 652 strategy (mean percentage +/- SD) over the last 5 000-time steps. For (a) and (d) the intensity
 653 of black represents the proportion of each strategy for the given time. It is log-transformed for
 654 (d). For (b) and (e) grey patches are unsuitable, white patches are suitable and empty, and
 655 coloured patches are suitable and occupied by populations differing in dispersal strategies
 656 (ranging from low dispersal in red to high dispersal in blue). Dispersal strategies are similarly
 657 color coded in panels (c) and (f). The first row of panels (a-c) shows an example with two
 658 equally abundant dispersal distance strategies (dispersing at 5 and 9 patches). Conditions are
 659 fragmentation of 99% and no aggregation. The second row of panels (d-f) shows an example
 660 where one dispersal distance strategy (at 1.1 patches) dominates (fragmentation of 95% and
 661 aggregation of 20%).

662



663

664 **Figure 4:** Fragmentation level leading to the metapopulation extinction versus mutation rate
 665 for different scenarios of fragmentation rate and aggregation. Orange arrows highlight the
 666 difference of extinction thresholds between no evolution and fast evolution, a proxy for
 667 maximal evolutionary rescue. Blue arrows highlight the change in mutation rate that has a
 668 maximal effect on evolutionary rescue. Note that this occurs when mutation rates become
 669 roughly ten times higher than fragmentation rates (a-c). Evolutionary rescue is largely
 670 decreased in aggregated landscapes (d-f).

671