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# Evolution of dispersal and the maintenance of fragmented metapopulations

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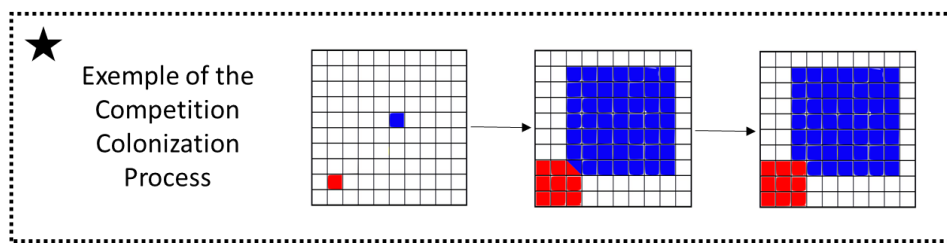
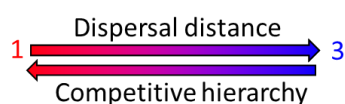
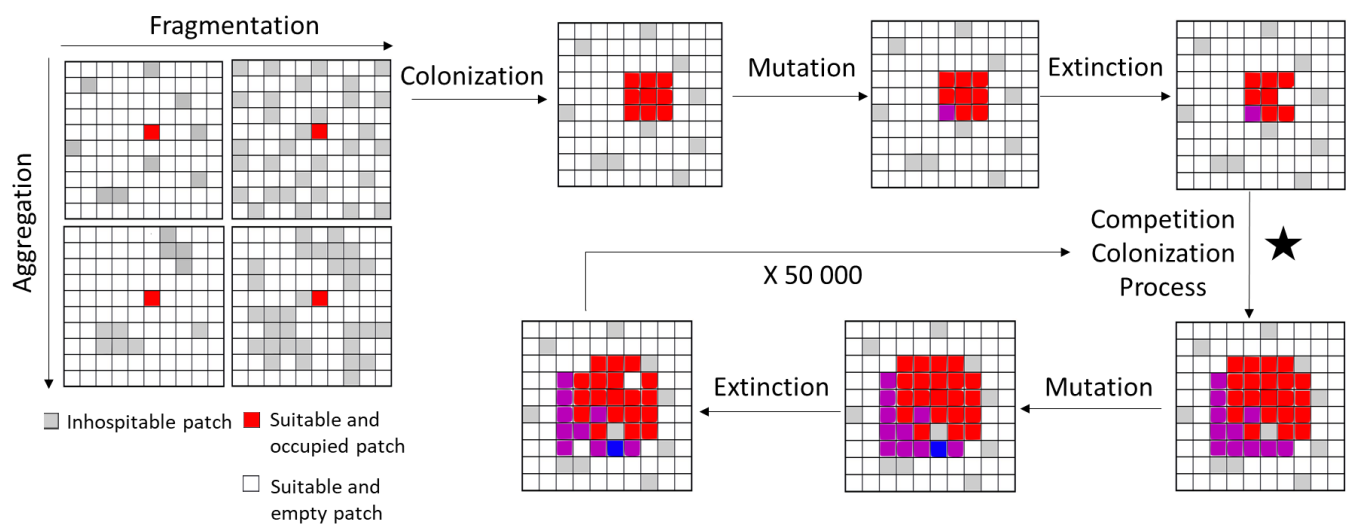
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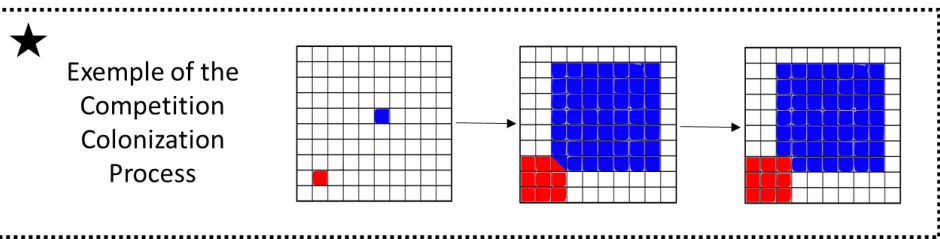
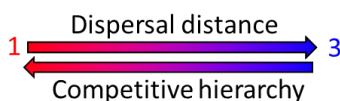
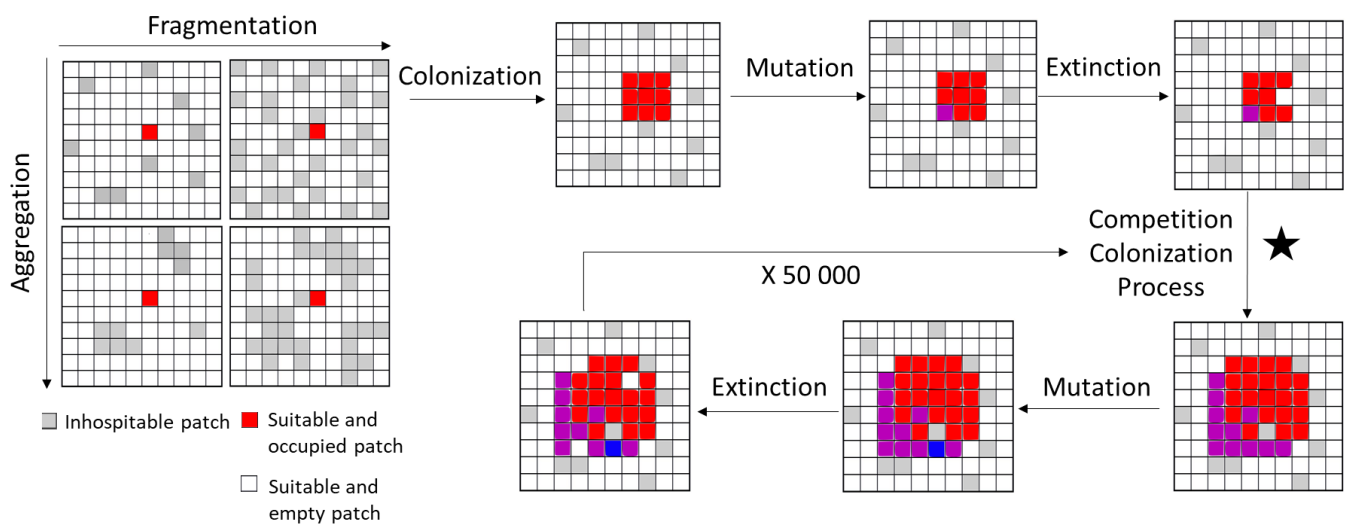
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1 **ABSTRACT:**

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



17 changing environments.

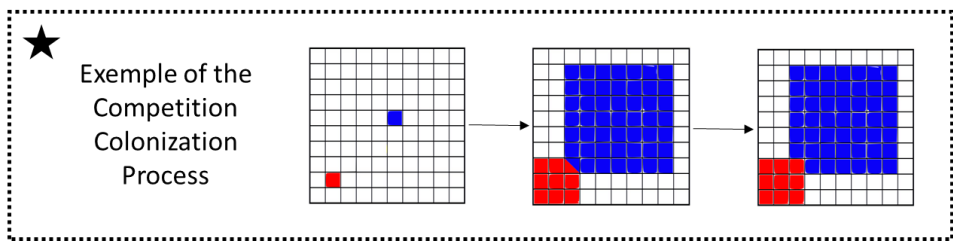
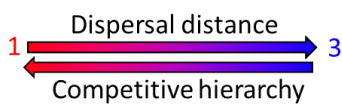
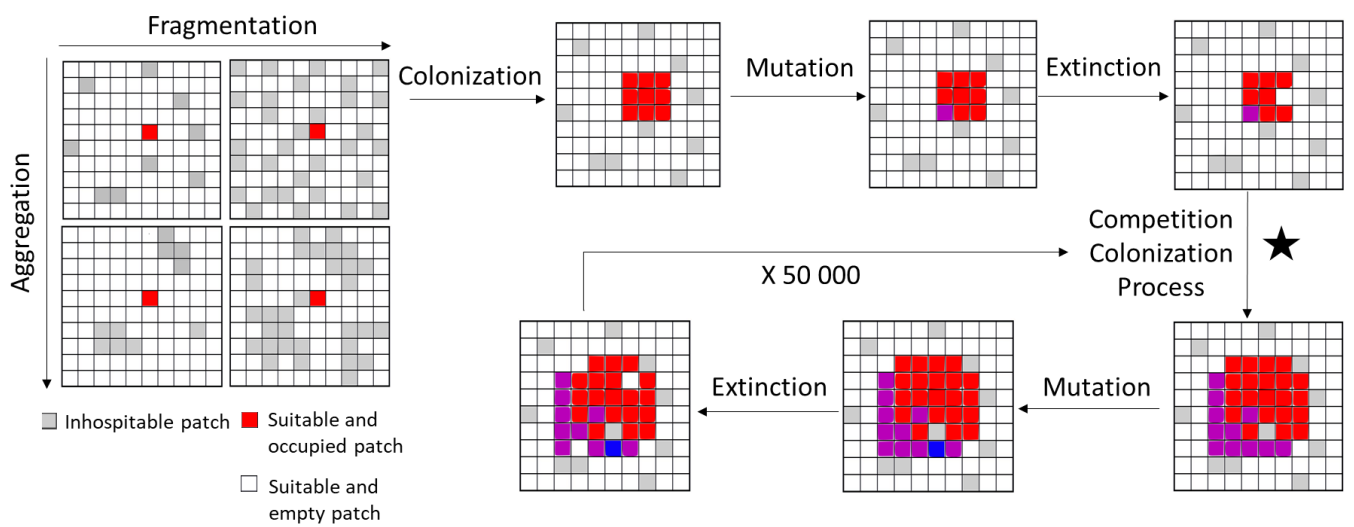
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19 **Keywords:** Dispersal evolution, fragmentation, metapopulation, evolutionary rescue, spatial

20 autocorrelation

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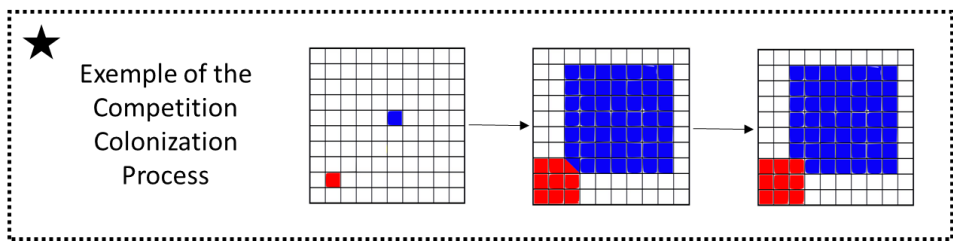
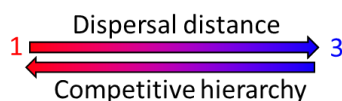
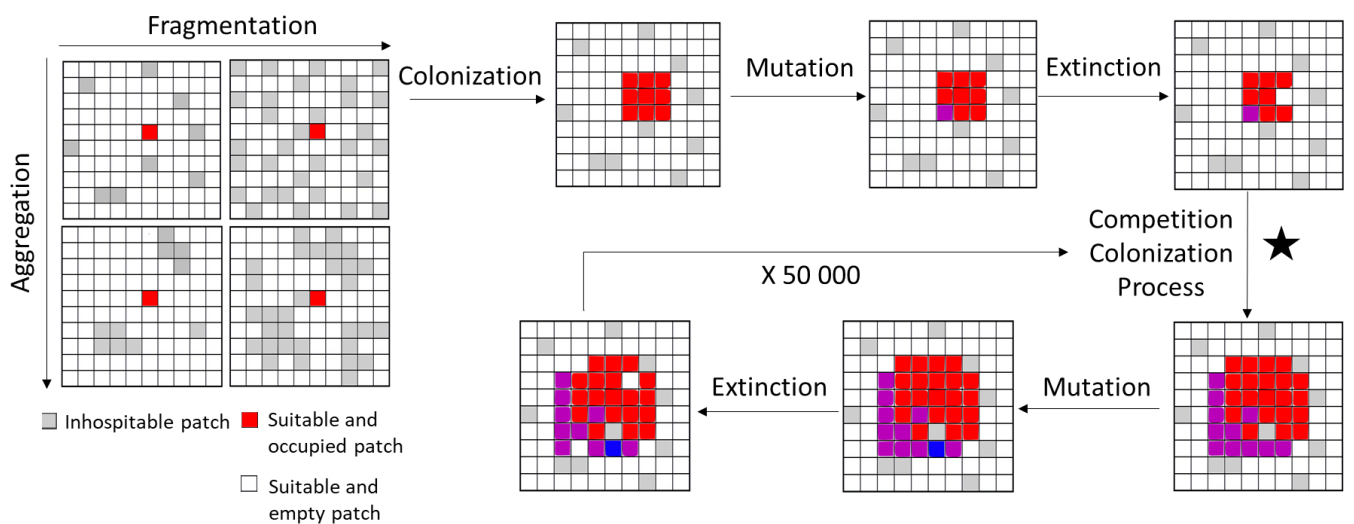
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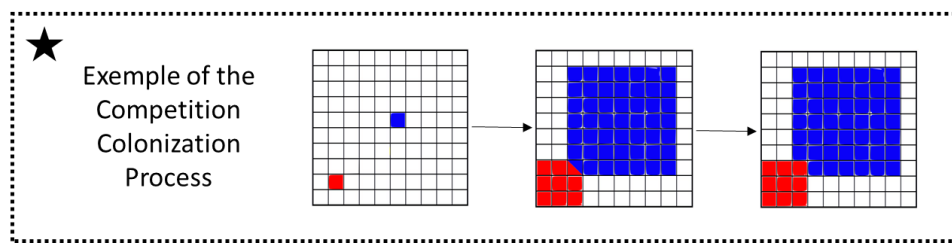
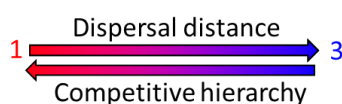
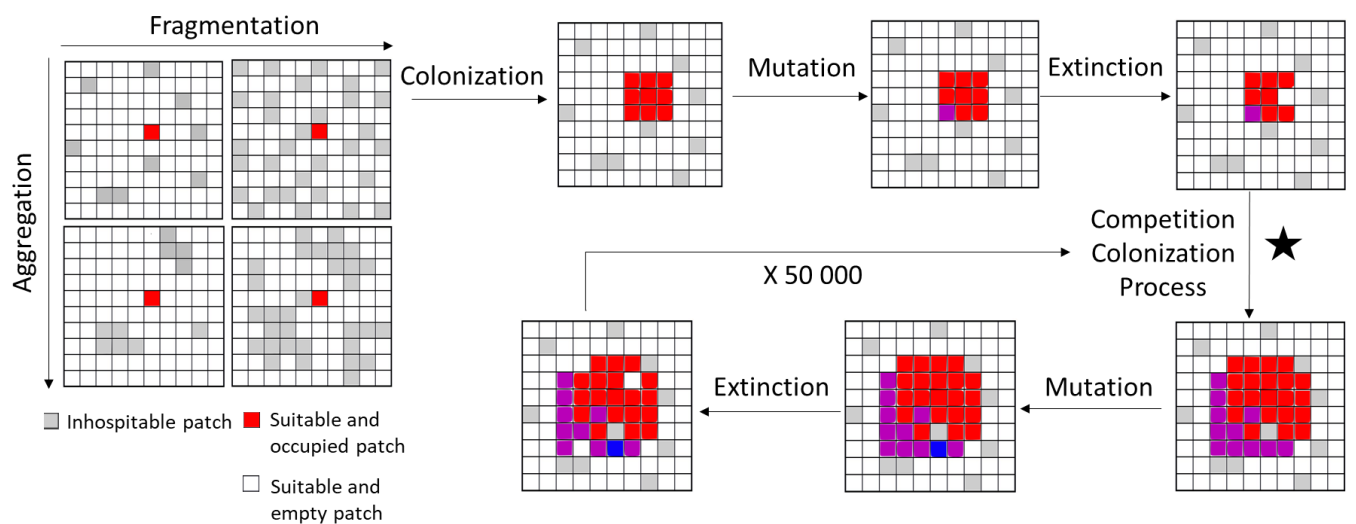
23 **INTRODUCTION**

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

38 Habitat fragmentation creates spatial heterogeneities in several ways. It decreases the

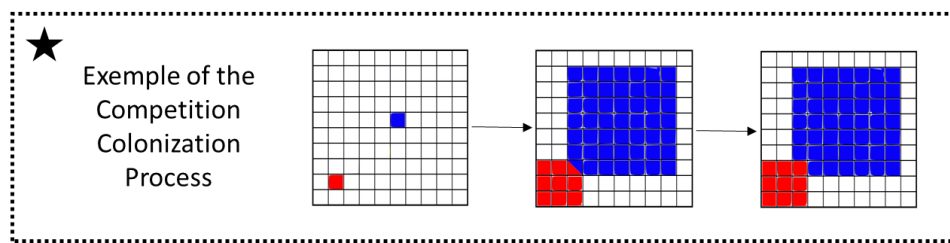
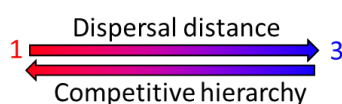
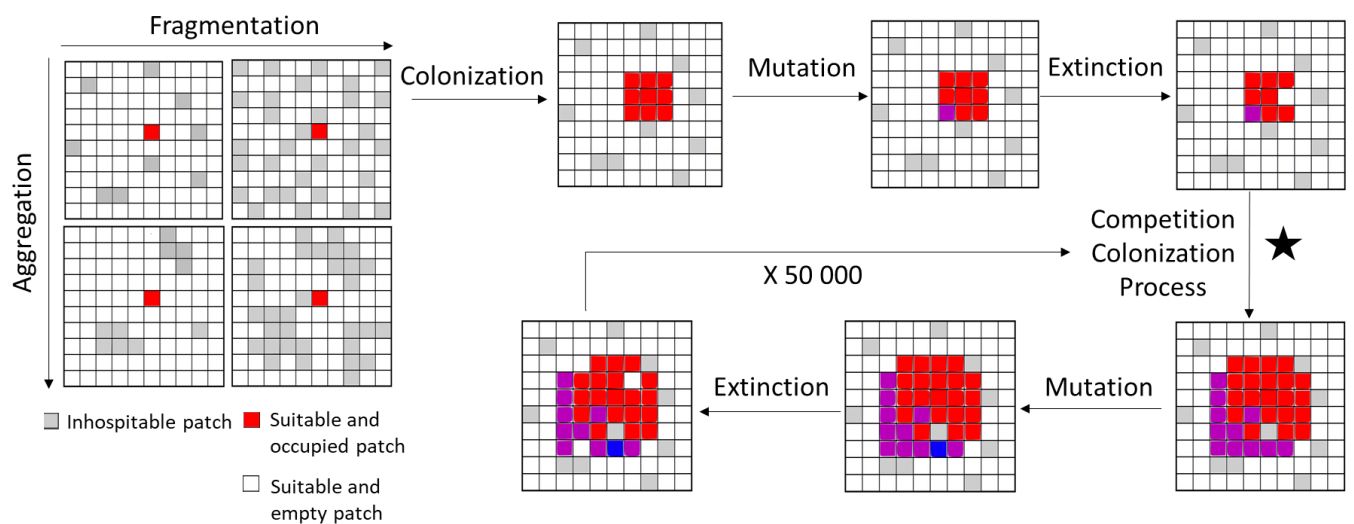


39 quantity of suitable habitat by decreasing the size and increasing the isolation of suitable  
 40 patches, even though it increases their number (Fahrig 2003). In our study, fragmentation is  
 41 defined by the proportion of hostile vs. suitable locations (patches) and we systematically  
 42 vary its degree of spatial aggregation. Dispersal evolution is affected by fragmentation, due to  
 43 variations of different selective pressures. By definition, fragmentation increases spatial  
 44 heterogeneity so that dispersing propagules encounter non-suitable patches more frequently.  
 45 Theoretical and empirical studies suggest that such increases in dispersal costs and in spatial  
 46 heterogeneity select decreased dispersal (Hastings 1983, Travis and Dytham 1999,  
 47 Schtickzelle et al. 2006, Bonte et al. 2006, Cheptou et al. 2008, Duputié and Massol 2013).  
 48 While such a counterselection of dispersal was originally highlighted in theoretical models  
 49 (Hastings 1983, Travis and Dytham 1999), empirical evidence for such effects has  
 50 accumulated in recent years, for a large variety of species, from the weed *Crepis sancta*  
 51 (Cheptou et al. 2008), to the butterfly *Proclissiana eunomia* (Schtickzelle et al. 2006) and the  
 52 wolf spider *Pardosa monticola* (Bonte et al. 2006). Habitat fragmentation however also  
 53 increases inbreeding, kin competition or temporal variation of the environment and all of  
 54 these components usually select for higher dispersal abilities (Hamilton and May 1977,  
 55 Charlesworth and Charlesworth 1987, Matthysen et al. 1995, Gandon 1999, Duputié and

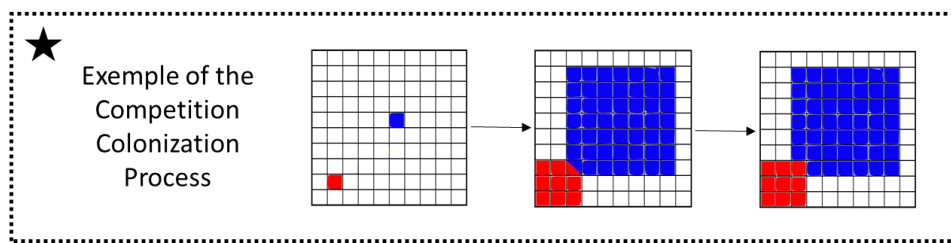
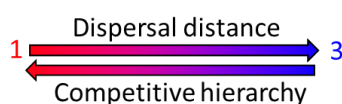
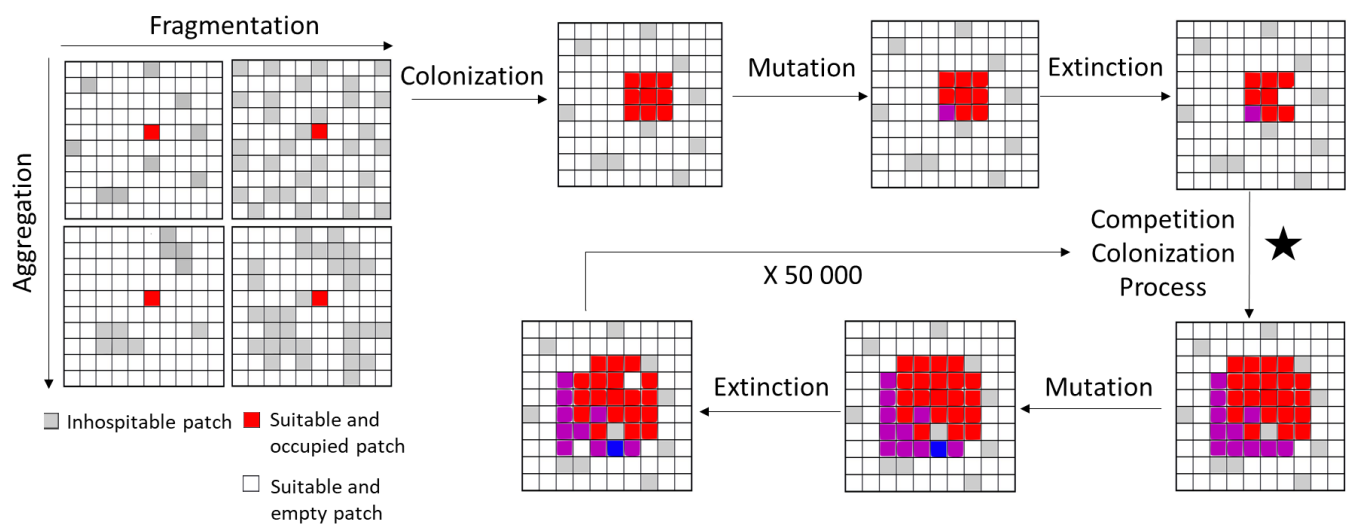


56 Massol 2013, Cote et al. 2017, Tung et al. 2018, Oldfather et al. 2021). In addition to the  
 57 modulation of overall dispersal levels, fragmentation can also, under certain conditions,  
 58 maintain contrasted dispersal strategies simultaneously. Previous investigations suggest that  
 59 such a dispersal polymorphism evolves under high fragmentation and high aggregation, with  
 60 dispersing and non-dispersing individuals coexisting within the same population (Bonte et al.  
 61 2010). It principally appears because aggregation produces a coexistence of many small  
 62 patches and few large patches (Parvinen 2002, Massol et al. 2011, Parvinen et al. 2020), or  
 63 due to edge effects that select low dispersers at the edge and high dispersers in central places  
 64 (Travis and Dytham 1999).

65 While these previous studies consider dispersal as an isolated trait, it is now widely  
 66 recognized that evolutionary changes in dispersal most often imply variations in phenotypic  
 67 traits that constrain other ecological interactions (Raffard et al. 2022). It has been highlighted  
 68 that when colonization abilities (here our measure of dispersal) are traded against competitive  
 69 abilities, coexistence of a large number of strategies is possible along this hierarchy (Tilman  
 70 1994). This trade-off has a long history in ecology and former studies investigated how it may  
 71 explain the coexistence of species within metacommunities (Tilman et al. 1997, Yu and



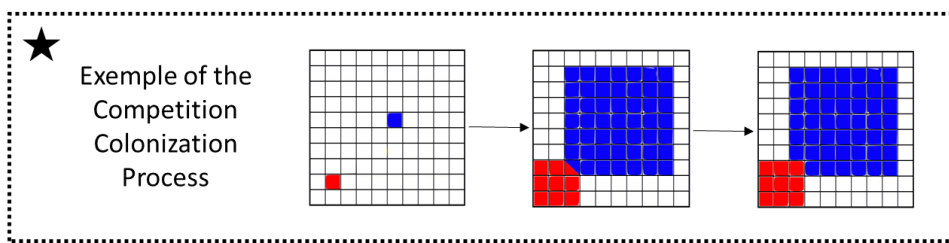
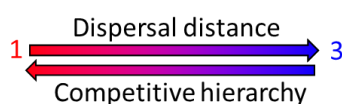
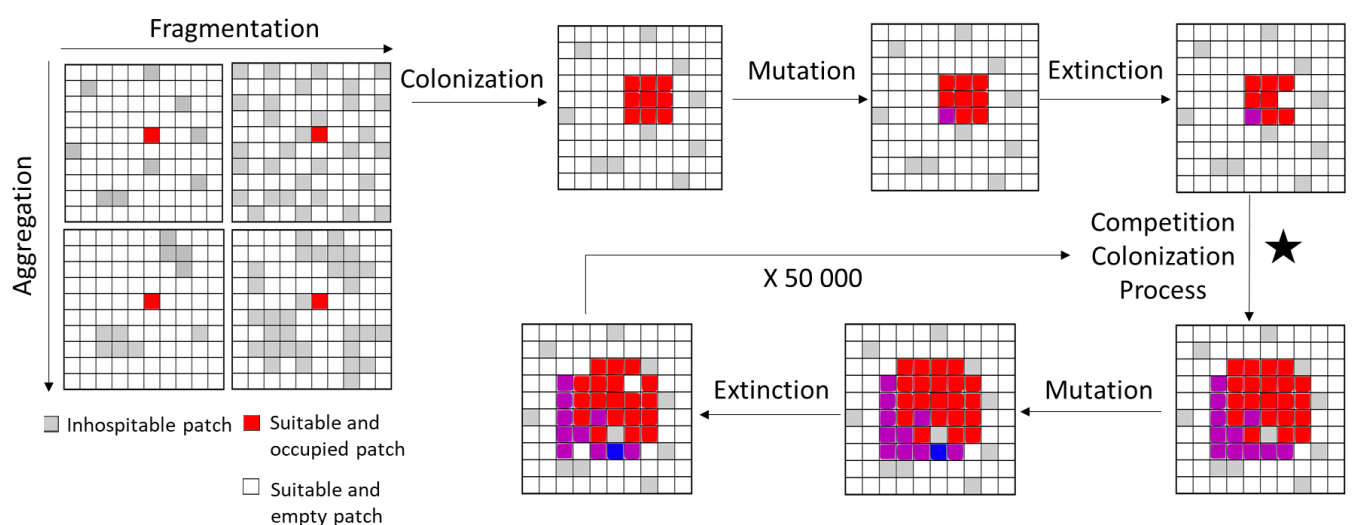
72 Wilson 2001, Calcagno et al. 2006) and how such a diversity varies when fragmentation or  
 73 habitat destruction occurs (Tilman et al. 1994, 1997). While these studies mostly focused on  
 74 ecological dynamics, we here use the trade-off to investigate its eco-evolutionary implications  
 75 in a fragmentation context. Such a trade-off could for instance occur because given a fixed  
 76 quantity of energy, allocation could produce a large number of small propagules (colonizer)  
 77 or few large propagules (competitor) (eg, Geritz et al., 1999; Smith & Fretwell, 1974). For  
 78 example, the weed *Crepis sancta* produces small and/or large seeds. Small seeds have high  
 79 wind dispersal due to their lightweight but low competitiveness due to low resource storage.  
 80 In contrast, large seeds have restricted dispersal due to their weight but contain more  
 81 resources (Cheptou et al. 2008). In social insects, dispersal and reproduction could follow  
 82 from the production of many isolated queens that fly large distances and have high mortality  
 83 or through the split of the colony in a few propagules that usually disperse on short distances  
 84 but may be more efficient at gathering resources when founding the new colonies (Cronin et  
 85 al. 2013, 2016). Habitat fragmentation affects strategies along the competition-colonization  
 86 trade-off in different ways. First, it directly lowers the average density at the metapopulation  
 87 level, thereby changing competitive pressures. Second, it creates isolated patches that act as a  
 88 positive filter for the best dispersers. To our knowledge, only one study considers how this





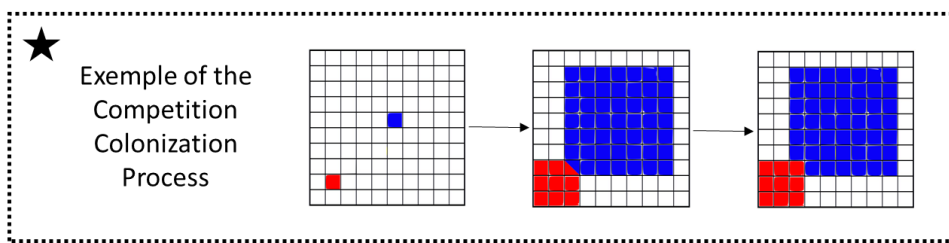
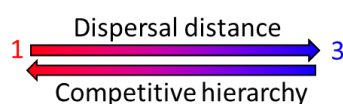
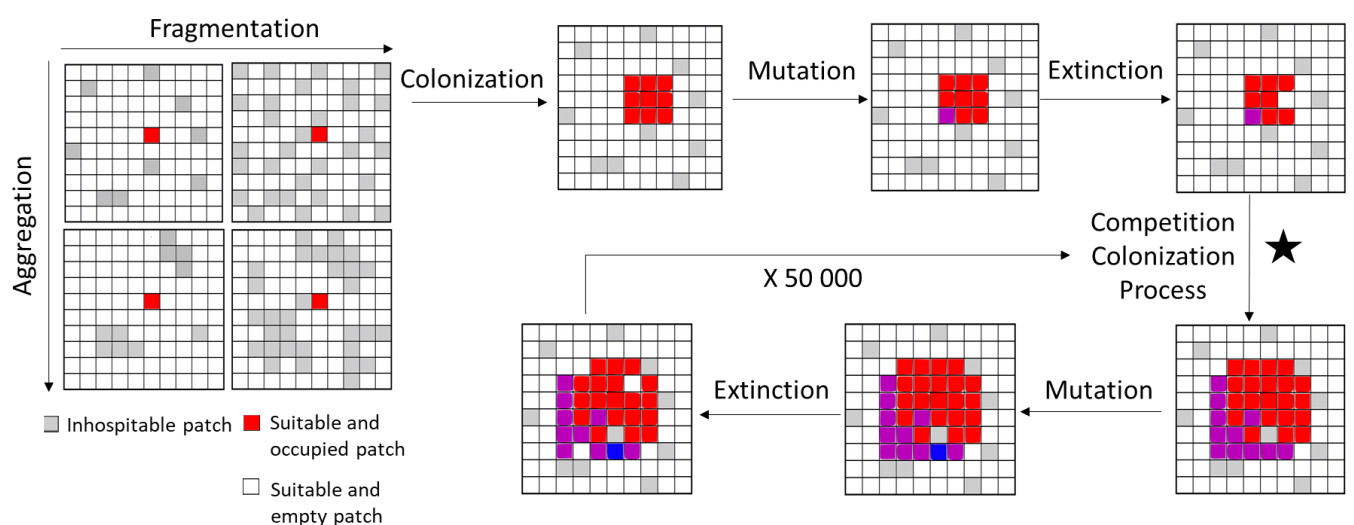
89 competition/colonization trade-off affects the dispersal strategies selected by fragmentation  
 90 (Tilman et al. 1994). This study shows that in a spatially variable environment with an  
 91 increase of fragmentation, the more competitive (and thus the less dispersive) strategies  
 92 disappear first, so that high dispersal strategies are selected.

93 Such results are obtained without considering explicit spatial structures as the position  
 94 of patches is not accounted for in Tilman et al. (1994) (mean field approximation).  
 95 Fragmentation of the environment can however be an aggregated process, as human activities  
 96 such as urban development or agricultural exploitation are often concentrated in specific  
 97 locations. A previous work on metapopulations shows that the structuration of habitat  
 98 heterogeneities is crucial to study metapopulation responses to fragmentation (Hiebeler 2000).  
 99 When environmental heterogeneities are spatially correlated (aggregation), predictions based  
 100 on mean-field approximation are often qualitatively incorrect when compared to spatially  
 101 explicit approaches (Hiebeler 2000). In contrast, mean-field approximations yield correct  
 102 results in the case of randomly distributed fragmentation. Leaving out the  
 103 competition/colonization trade-off, the importance of aggregation in the evolution of dispersal  
 104 is highlighted by various studies (Travis and Dytham 1999, Ovaskainen et al. 2002, Bonte et



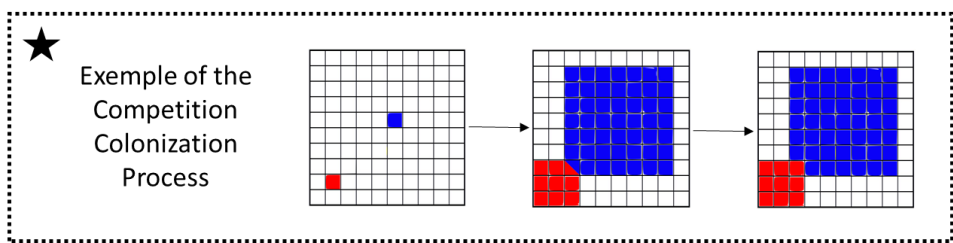
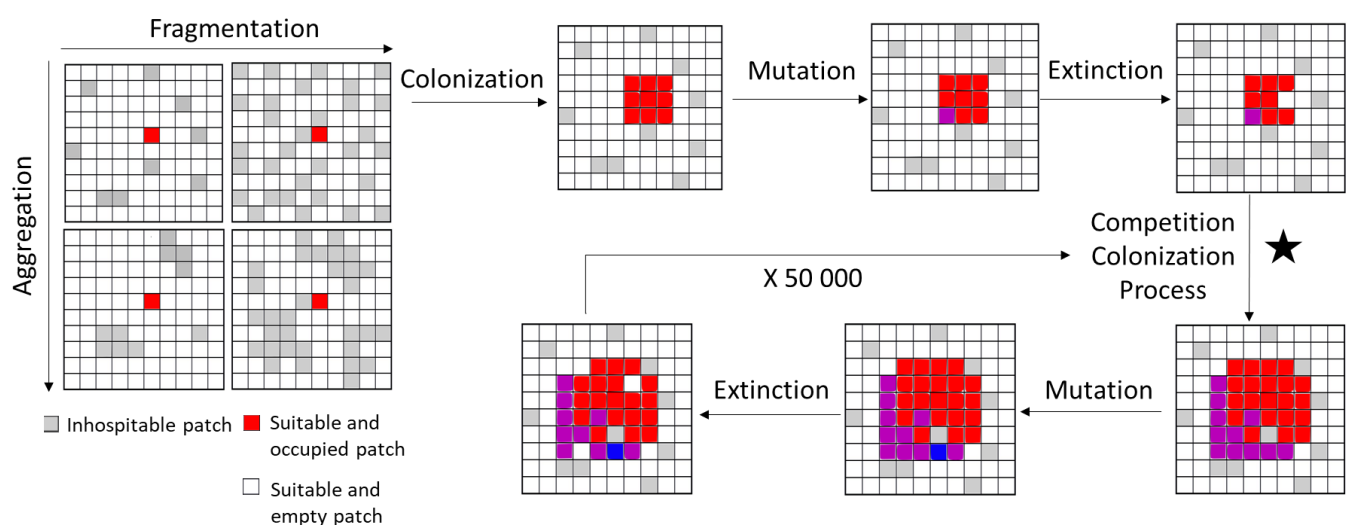
105 al. 2010, Fronhofer et al. 2014). For example, in the context of correlated extinctions,  
 106 empirical work on the spider mite *Tetranychus urticae* and an associated theoretical model  
 107 show a selection for long-distance dispersal and a decrease of local dispersal compared to  
 108 spatially random extinctions (Fronhofer et al. 2014). Travis and Dytham (1999) found a  
 109 decrease in dispersal with increased fragmentation, but an increase in dispersal with higher  
 110 aggregation. The risk to disperse outside of a large aggregate of suitable patches and into a  
 111 hostile environment is indeed lowered, so that aggregation modulates dispersal costs.  
 112 Similarly, Bonte et al. (2010) found a decrease of local and global dispersals with the increase  
 113 of fragmentation, and demonstrates that decreasing aggregation has the contrasted effect of  
 114 decreasing local dispersal and increasing global dispersal. To summarize, the study that  
 115 considers variations of dispersal strategies along a competition/colonization trade-off in  
 116 fragmented habitats use a spatially implicit (mean field) approach, while others use spatially  
 117 explicit landscapes but ignore possible competition/colonization trade-offs. The goal of our  
 118 study is therefore to integrate both aspects, that is to study the evolution of dispersal along the  
 119 competition/colonization trade-off given a spatially explicit structuration of the habitat.

120 Understanding this dispersal evolution has immediate consequences to better predict



121 the maintenance of metapopulations. For instance, a selected increase in dispersal favors the  
 122 exchange of individuals between patches and the colonization of empty patches (spatial  
 123 rescue). Extinction may also be prevented, by the emergence of evolutionary rescue, when  
 124 natural selection favors adapted traits (Gomulkiewicz and Holt 1995, Carlson et al. 2014, Bell  
 125 2017). Here, an evolutionary increase of dispersal distances could avoid a population  
 126 extinction in a climate change context (Boeye et al. 2012) or in a context of high mortality  
 127 (Heino and Hanski 2001). Given a temporally increasing fragmentation, natural selection may  
 128 favor high dispersal, as the availability of empty and isolated patches constantly increases.  
 129 Because only highly dispersive strategies can reach them, such isolated patches act as filters  
 130 that favor high dispersal (Heino and Hanski 2001). Consistent with this theoretical prediction,  
 131 a temporal increase of fragmentation led to higher dispersal in *Drosophila melanogaster*  
 132 experiments (Tung et al. 2018). Conversely, if evolution were to lead to less dispersal, it  
 133 would potentially decrease metapopulation persistence (Gyllenberg et al. 2002). The  
 134 implication of the evolution of dispersal for metapopulation persistence in a world that  
 135 becomes increasingly fragmented is therefore an important, unresolved issue.

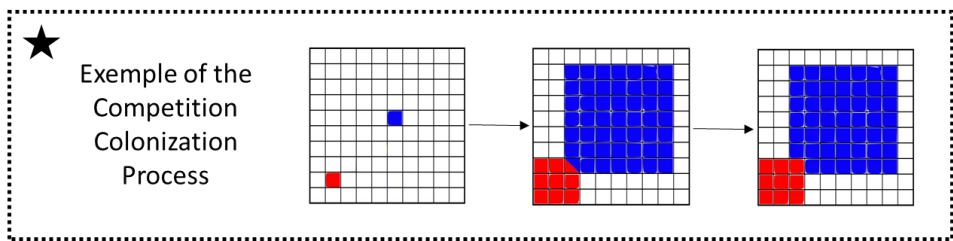
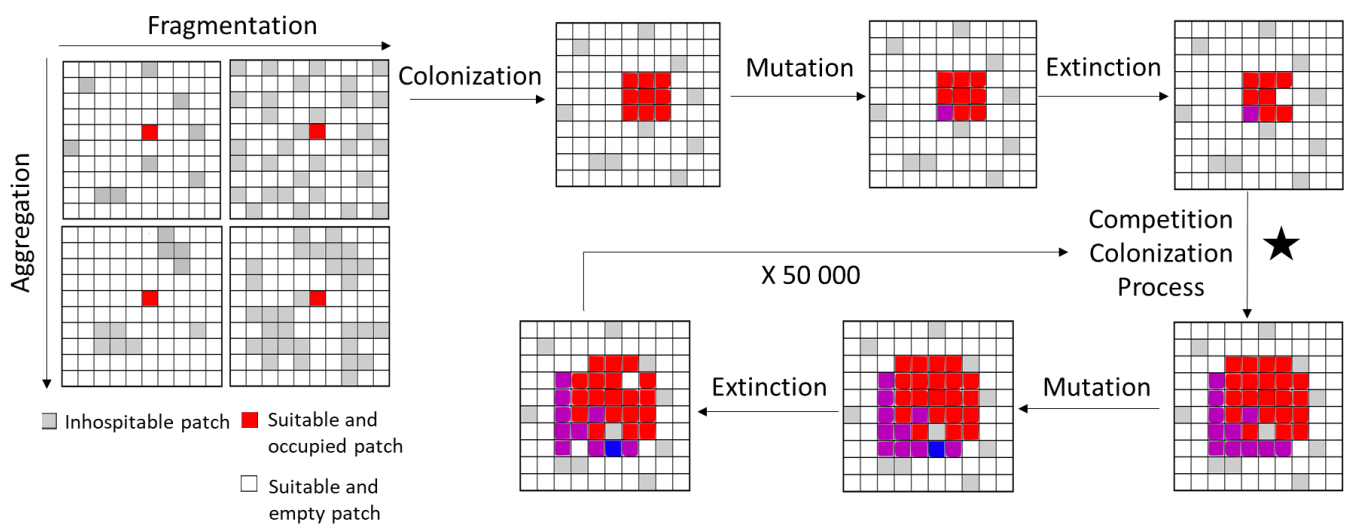
136 Using metapopulation simulations, we studied how the spatio-temporal structuration



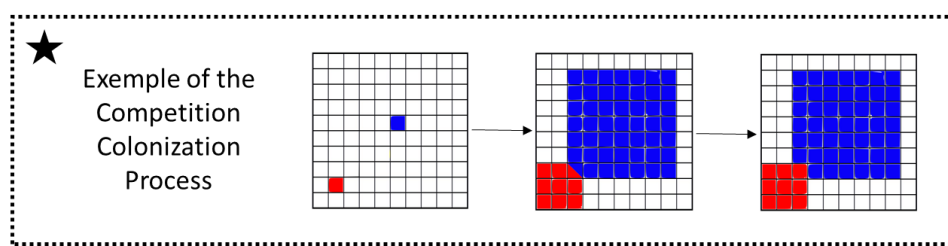
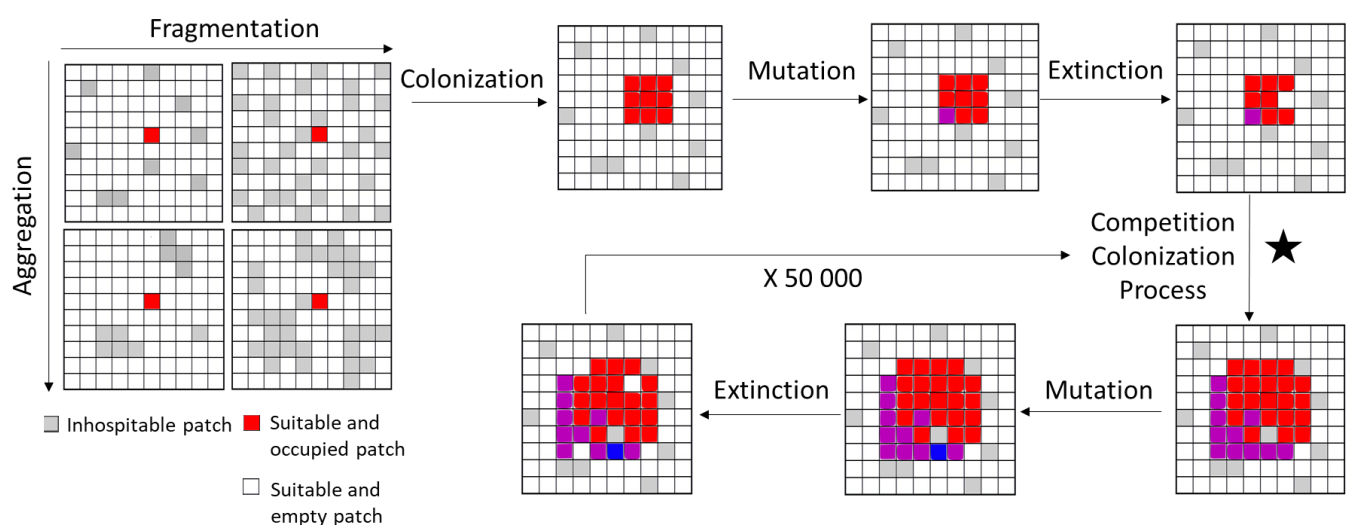
137 of fragmented environments acts on dispersal evolution given a competition/colonization  
 138 trade-off. First, we fixed fragmentation and aggregation levels and investigated how dispersal  
 139 evolved. Second, we varied fragmentation over time to test whether dispersal evolution can  
 140 prevent extinction (evolutionary rescue), under various rates of evolution of dispersal. We  
 141 hypothesize that, in a fixed environment, higher fragmentation selects for an increase in  
 142 dispersal because more empty patches will become available to colonizers and inaccessible to  
 143 competitors. In addition, competition could be relaxed in fragmented landscapes as the  
 144 average occupancy is lowered. However, if the fragmentation is aggregated, large groups of  
 145 suitable patches could persist in the landscape. Such a situation is favorable to competitors  
 146 and should decrease the selection toward higher dispersal or lead to dispersal polymorphism  
 147 with competitors dominating aggregated patches while colonizers remain favored in isolated  
 148 patches. When fragmentation increases over time, we hypothesize that the occurrence of  
 149 evolutionary rescue depends on the speed of evolution of dispersal, which needs to be faster  
 150 than the speed of fragmentation to counterbalance its effects.

151

152 **MODEL PRESENTATION**



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

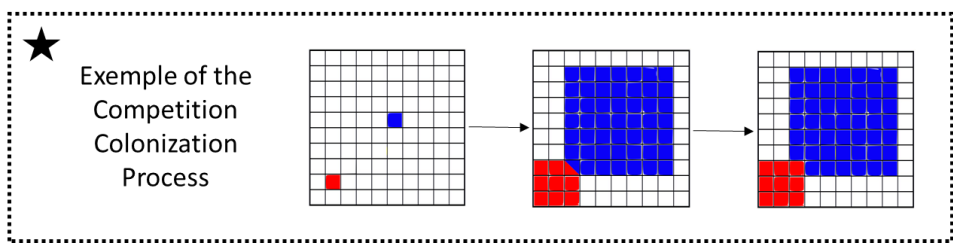
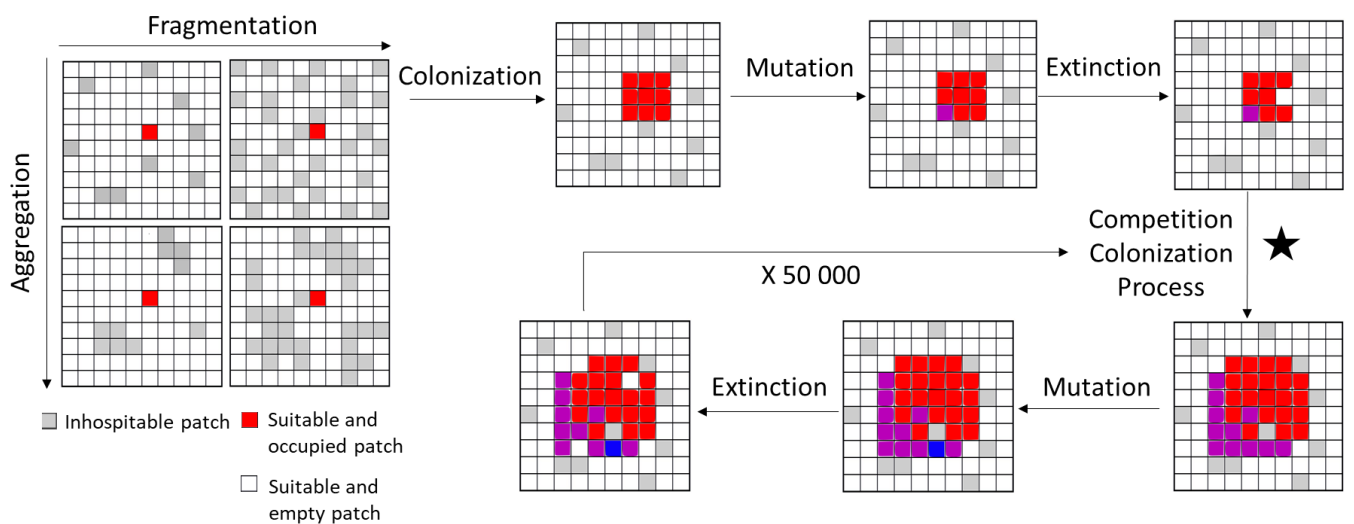


170 A higher aggregation means that a suitable patch is more likely to be close to another one  
 171 compared to the random expectation.

172 Individuals are characterized by two traits: colonization and competition capacities  
 173 (both integer values) directly linked through the colonization/competition trade-off. The  
 174 model relies on discrete time steps, each time step being divided in three parts: colonization,  
 175 competition and extinction (see Fig. 1).

176 (1) Colonization. The colonization capacity defines the radius (number of patches) of the  
 177 area around the individual where its offspring are dispersed. We assume that offspring  
 178 will potentially colonize all empty but suitable patches within this range. Because all  
 179 patches within the radius are colonized if empty, it also means that strategies that have  
 180 a higher dispersal range can potentially yield more offspring (i.e. be more fecund) than  
 181 strategies that are less dispersive.

182 (2) Competition. We assume that only empty suitable patches can be colonized by  
 183 propagules. Given that individuals fill all suitable surrounding patches with their  
 184 offspring, suitable empty patches are often reached by several offspring  
 185 simultaneously. We then assume that the competitive hierarchy favors the strategy that









218

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

220 In the second scenario, we progressively increase the level of fragmentation over time.

221 We systematically manipulate the rates of fragmentation and of mutation to investigate

222 conditions under which dispersal evolution can delay extinction. The grid is supposed to be

223 fully suitable at the onset of the simulation and for the first 200-time steps. We then

224 progressively increase fragmentation until the metapopulation becomes extinct. As in the first

225 scenario, the increase in fragmentation occurs with random or aggregated distributions of

226 unsuitable patches (levels of aggregation: 0%, 10%, 20%, 40%, 60%, 80%). Rates of

227 fragmentation correspond to the probability that a suitable patch becomes unsuitable within a

228 given time step. We tested three rates of fragmentation (0.0001, 0.001, 0.01). As evolutionary

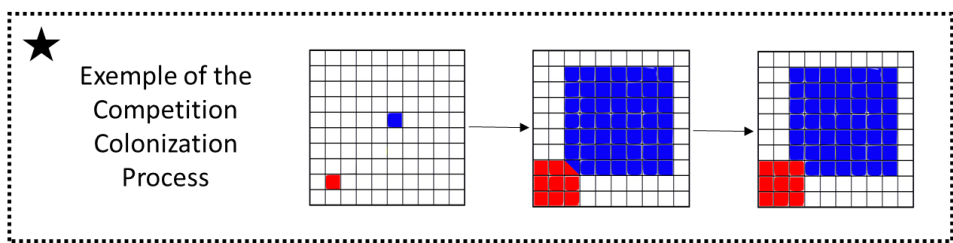
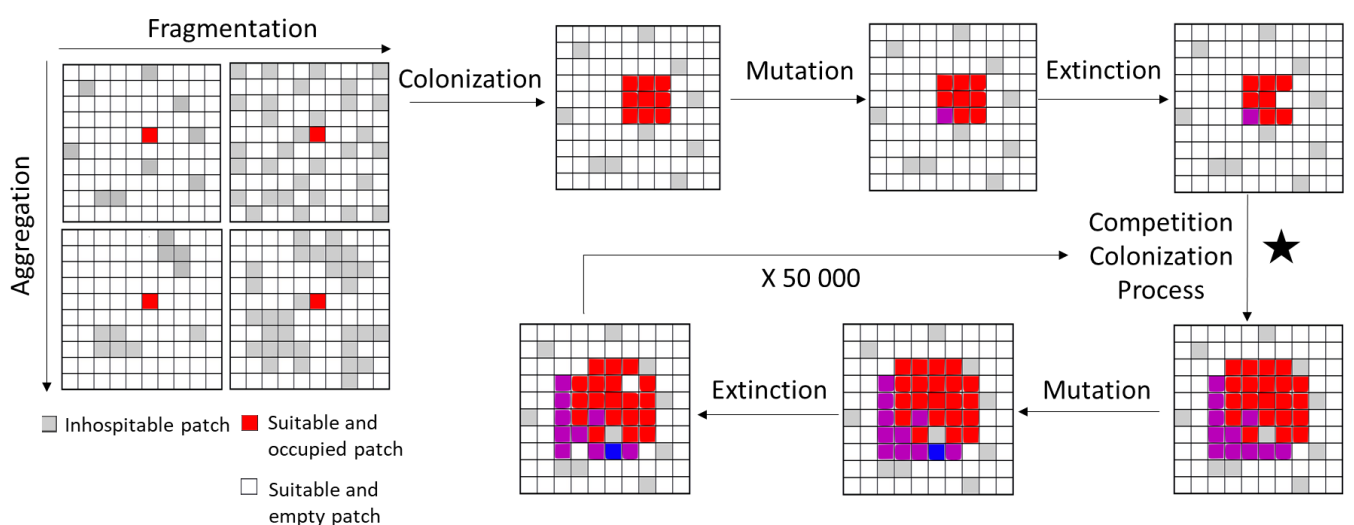
229 rescue is construed as a race between the speed of the disturbance and the speed of adaptation

230 (Gomulkiewicz and Holt 1995), we also systematically manipulate the speed of evolution by

231 considering different rates of mutation (0.001, 0.01, 0.1). We replicate each combination of

232 aggregation, fragmentation rate and mutation rate forty times. We record the fragmentation at

233 population extinction as an index of the resistance of the metapopulation to the disturbance.



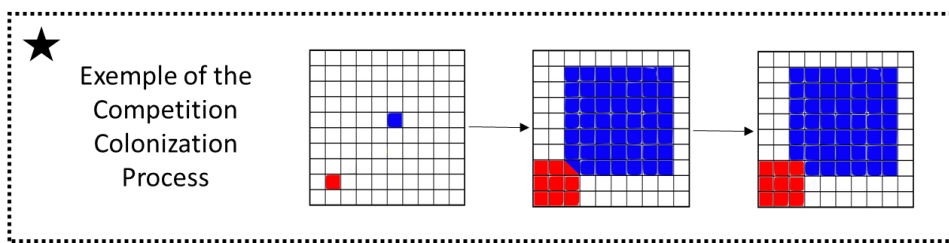
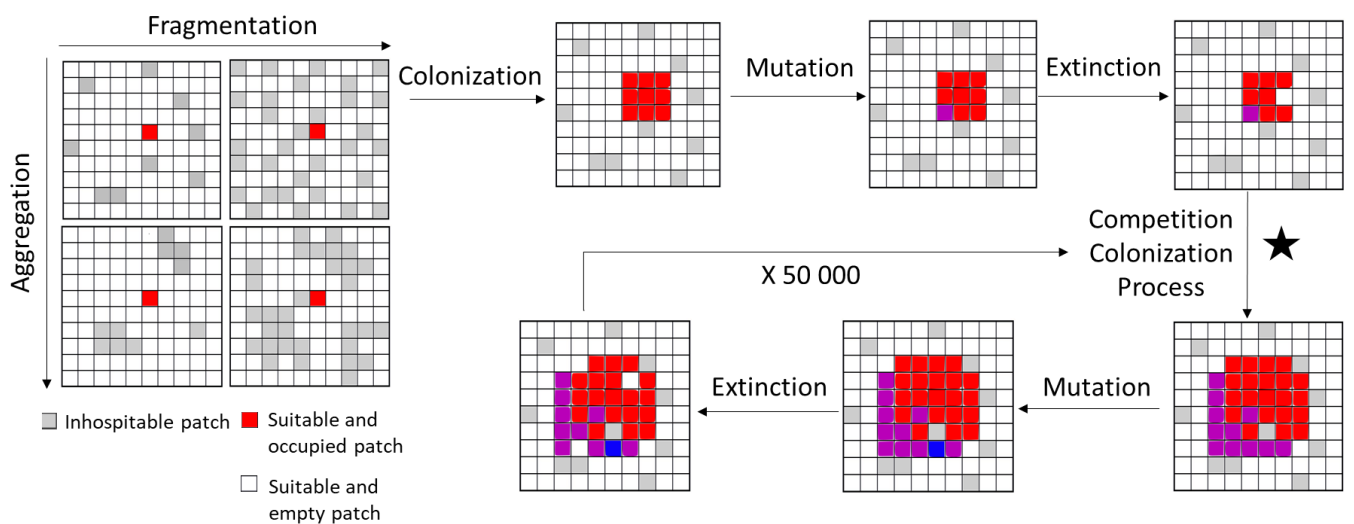
234 Higher values of this index show that evolution of dispersal allowed the metapopulation to  
 235 survive higher levels of the disturbance. Evolutionary rescue occurs if metapopulations with  
 236 evolution of dispersal resist higher disturbance levels than metapopulations without dispersal  
 237 evolution. For each set of simulations, we also record the variations of dispersal strategies  
 238 (occupancy of the various dispersal phenotypes) over time to identify the path that  
 239 evolutionary rescue takes.

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## 241 RESULTS

### 242 *Evolution of dispersal in fixed fragmented landscapes*

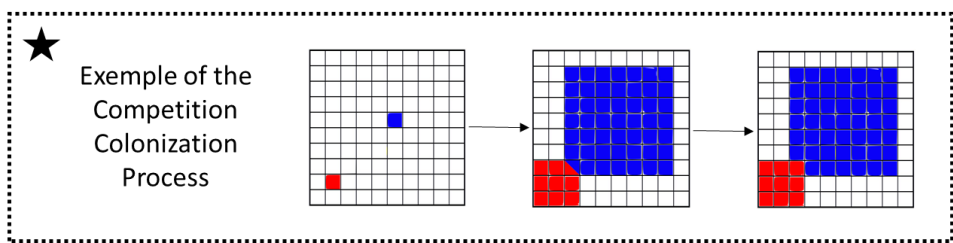
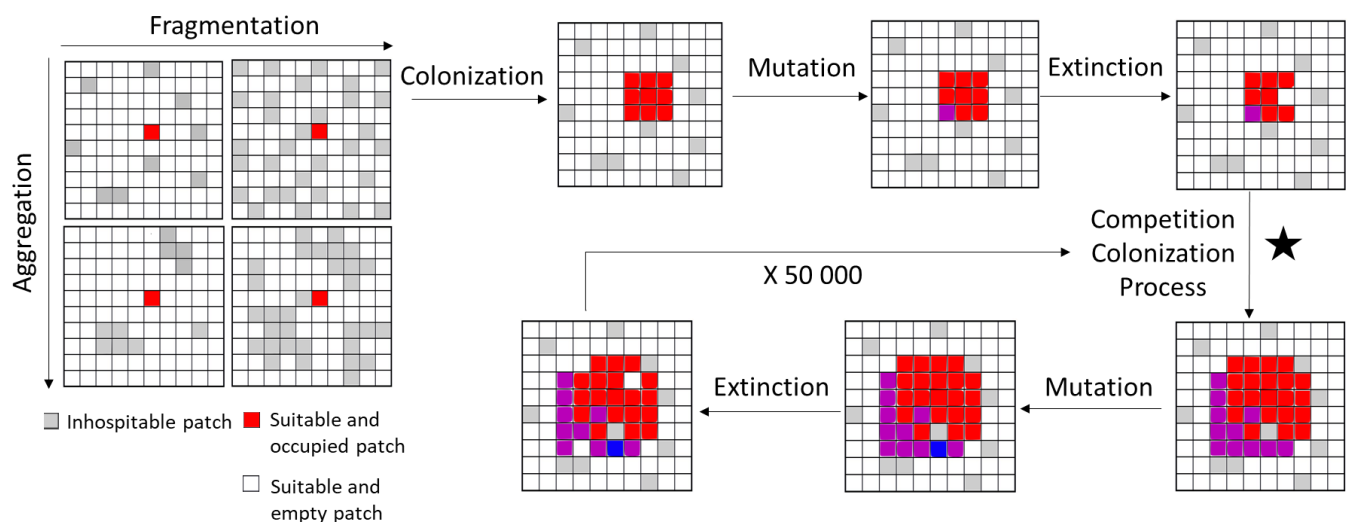
243 Higher fragmentation selects for increasing mean dispersal distances. In non-  
 244 fragmented landscapes, competitive strategies eventually dominate so that dispersal distance  
 245 quickly evolves close to one (Fig. 2a and b). Such a strategy remains dominant for all low  
 246 levels of fragmentation (0 to 60%). High dispersal is selected under higher fragmentation,  
 247 especially strongly when fragmentation is random ( $7.27 \pm 1.08$  patches at 99%, red line in Fig.  
 248 2a, see also Fig. 2c). However, adding aggregation strongly decreases this selection effect.



249 For instance, a little bit of aggregation (20%, orange line in Fig. 2a, see also Fig. 2d) suffices  
 250 to lower the selected dispersal distance in very fragmented landscapes to  $2.09 \pm 1.02$  patches.  
 251 Higher aggregation (40 to 80%) further decreases the selected dispersal distance, so that  
 252 fragmentation hardly has any effect on selected dispersal when aggregation is high (blue lines,  
 253 Fig. 2a). Aggregation therefore qualitatively changes the results of mean field models (such as  
 254 Tilman et al., 1994).

255 *Evolution of polymorphism in fragmented landscapes.*

256 Beyond the observed variations in mean dispersal distances, the long-term variability  
 257 of dispersal strategies also depends on fragmentation and aggregation. Particularly, when  
 258 fragmentation is sufficient, we observe the coexistence of several dispersal strategies  
 259 (polymorphism, Fig. 3). In all cases of polymorphisms, we observe similar patterns. Suitable  
 260 patches that are close to one another sustain the less dispersive strategies, while isolated  
 261 patches act as filters that favor the more dispersive strategies. The set of polymorphic  
 262 strategies however vary depending on the relative positions of patches. For instance, given a  
 263 very high fragmentation (99%) with no or little aggregation (20% or less), few suitable  
 264 patches are close to one another by chance (purple patches, Fig. 3b). Because the distances

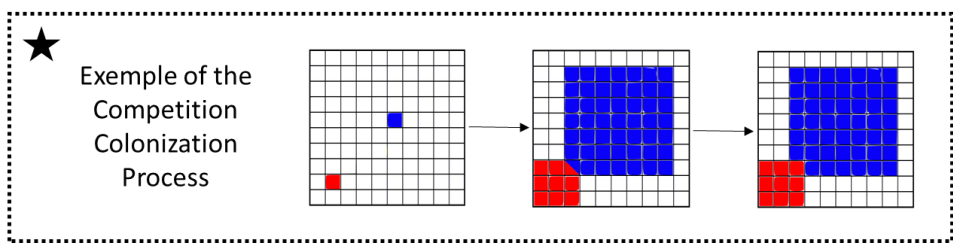
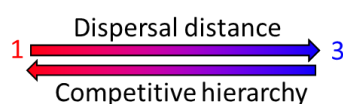
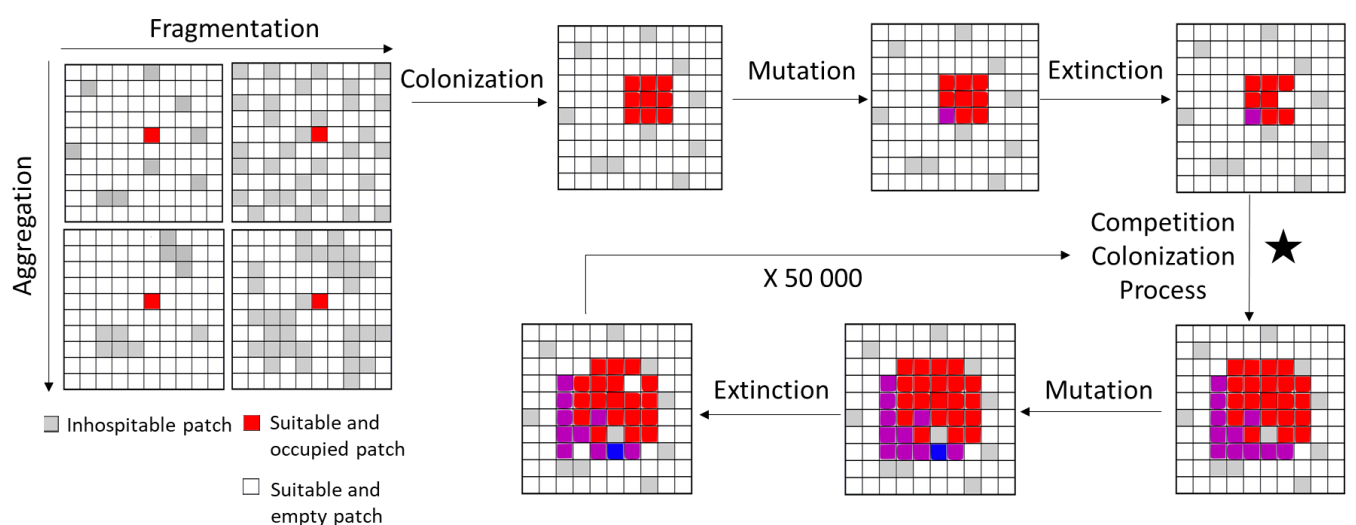


265 among these patches is still quite important, the dispersal strategy they sustain is still quite  
 266 high (around 5). Other patches are more isolated (blue patches, Fig. 3c) and act as a selective  
 267 pressure favoring very high dispersal distances (around 9). When fragmentation is slightly  
 268 lower (80 to 95%) and aggregation slightly higher (20 to 40%), large aggregates of suitable  
 269 patches occur in the landscape (red patches, Fig. 3e) and favor competitive strategies  
 270 (dispersal distance around 1). The remaining suitable patches are isolated and favor a  
 271 continuum of more dispersive strategies.

272

273 *Evolutionary rescue under progressively increasing fragmentation*

274 When fragmentation increases over time, fast dispersal evolution allows a longer  
 275 persistence of the metapopulation, i.e. an evolutionary rescue. Fig. 4 shows this evolutionary  
 276 rescue as the difference (orange arrows) between the scenario with no evolution (mutation  
 277 rate equal zero) and the three scenarios with more or less rapid evolution. Intuitively,  
 278 evolutionary rescue occurs and is strongest when there is no aggregation, fragmentation rate is  
 279 low, and mutation rate is high (mean difference of 3.04% between scenarios without and with  
 280 evolution, Fig. 4a). Evolutionary rescue is largely decreased when fragmentation rate is

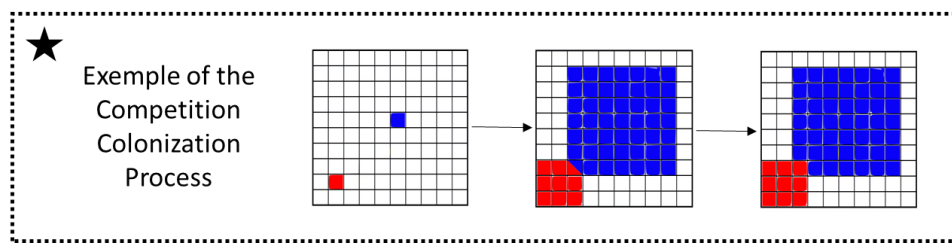
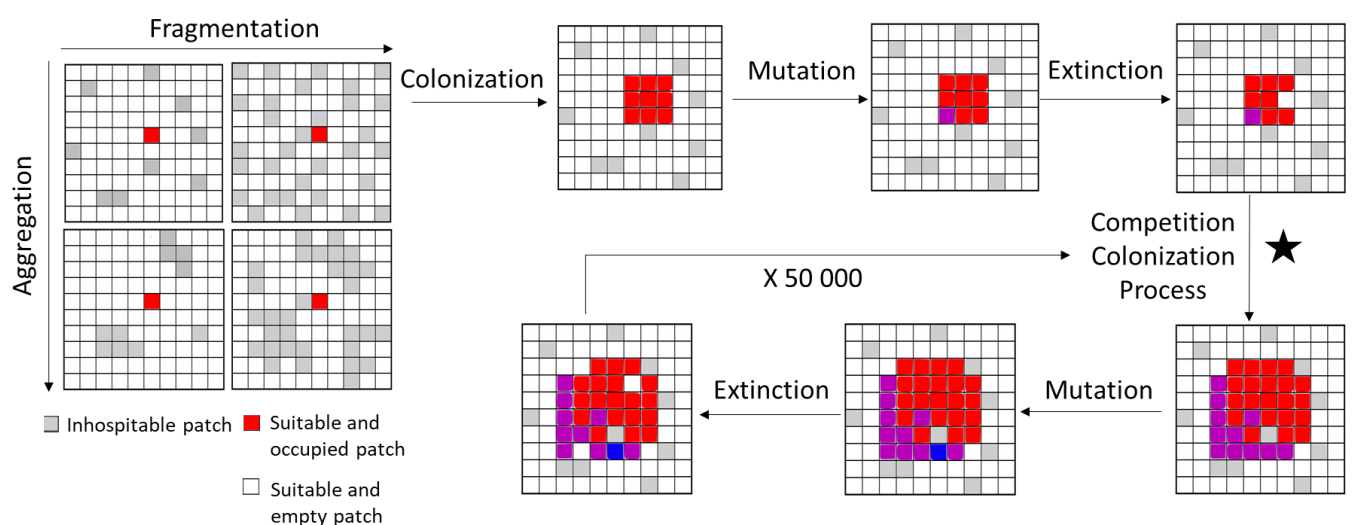


281 higher (a difference of 0.63%, Fig. 4c). Variations in the potential of evolutionary rescue are  
 282 not continuous. Rather, a jump in the extinction time when mutation rates increase can be  
 283 identified. This jump is relative to the fragmentation rate. Under our set of parameter values,  
 284 evolutionary rescue occurs when the mutation rate is ten times higher than the fragmentation  
 285 rate (Fig. 4a,b,c, blue arrows). Finally, we stress that aggregation largely constrains  
 286 evolutionary rescue. No potential for evolutionary rescue can be identified in aggregated  
 287 landscapes (Fig. 4d,e,f).

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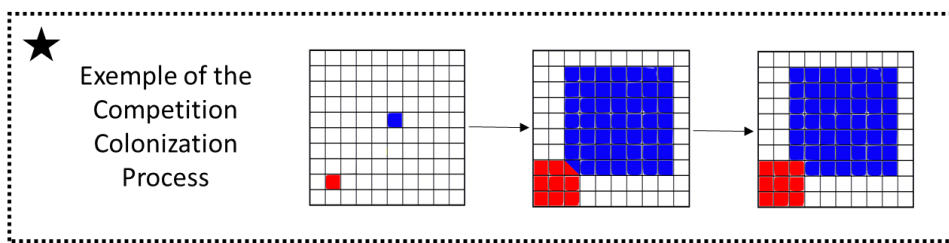
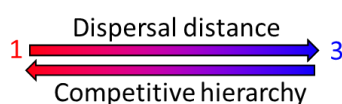
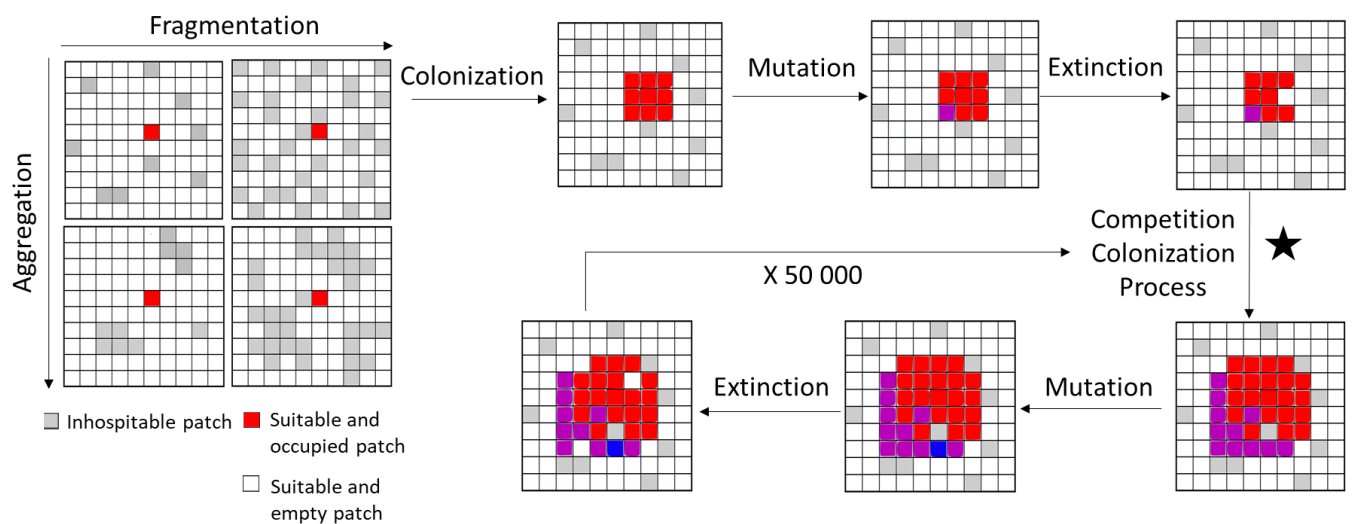
## 289 DISCUSSION

290 Our study shows an increase of dispersal capacities in fragmented landscapes in the  
 291 context of competition/colonization trade-offs. It not only highlights how such a trade-off  
 292 may affect the direction of dispersal evolution in the context of fragmentation, but also shows  
 293 that an explicit modeling of the spatial context potentially leads to vastly different outcomes  
 294 compared to mean field approaches. This importance of an explicit spatial context is in line  
 295 with previous theoretical studies of fragmented metapopulations (Gros et al. 2006, Poethke et  
 296 al. 2011, Henriques-Silva et al. 2015). Aggregation acts as an opposite force, as decreased



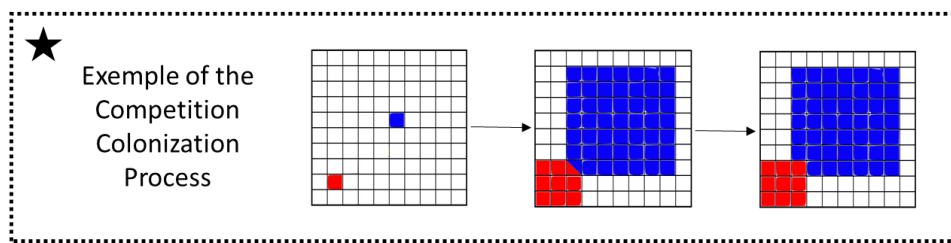
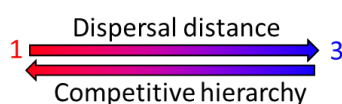
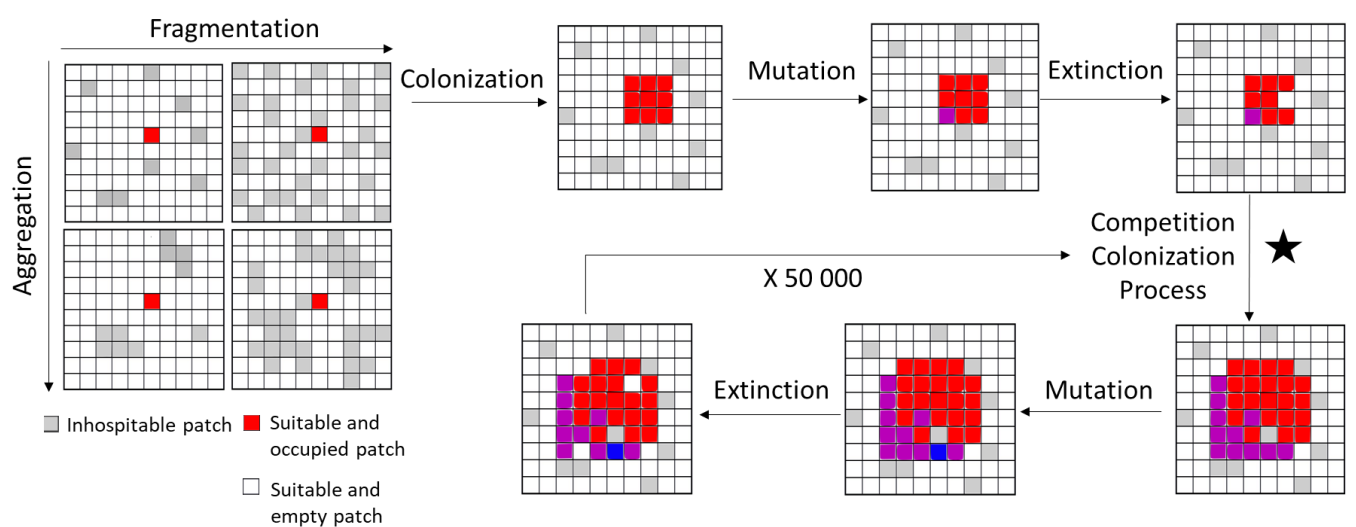
297 dispersal is selected in more aggregated landscapes. At high fragmentation and low  
 298 aggregation, different strategies can be selected and can coexist, with better competitors in  
 299 aggregated patches and better colonizers in isolated patches. Such an evolution of  
 300 polymorphism allows a good global coverage of available space. When fragmentation  
 301 increases with time, the rapid evolution of dispersal facilitates the survival of the  
 302 metapopulation but this evolutionary rescue effect can only be observed in non-aggregated  
 303 landscapes and when fragmentation rate is not too high.

304 The selection of more dispersive strategies in fragmented landscapes in a context of  
 305 competition/colonization trade-offs is congruent with Tilman et al. (1994) which also relies  
 306 on this trade-off. Other studies on the evolution of dispersal in spatially heterogeneous  
 307 systems, but in the absence of a competition/colonization trade-off, show a reverse pattern, as  
 308 dispersal is then counter selected because dispersal costs are enhanced by spatial  
 309 heterogeneities (Hastings 1983, Travis and Dytham 1999, Gros et al. 2006, Poethke et al.  
 310 2011). At the extreme such studies even propose that increases in spatial heterogeneities, for  
 311 instance to local habitat improvement, may result in the metapopulation demise (Poethke et  
 312 al. 2011). The difference between these studies and ours highlights how patterns of selection



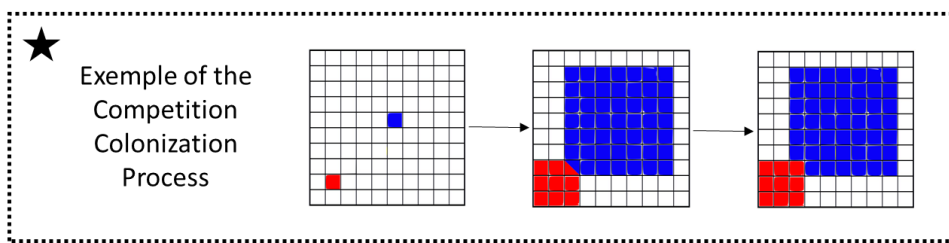
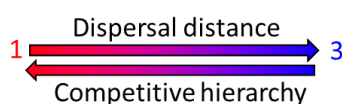
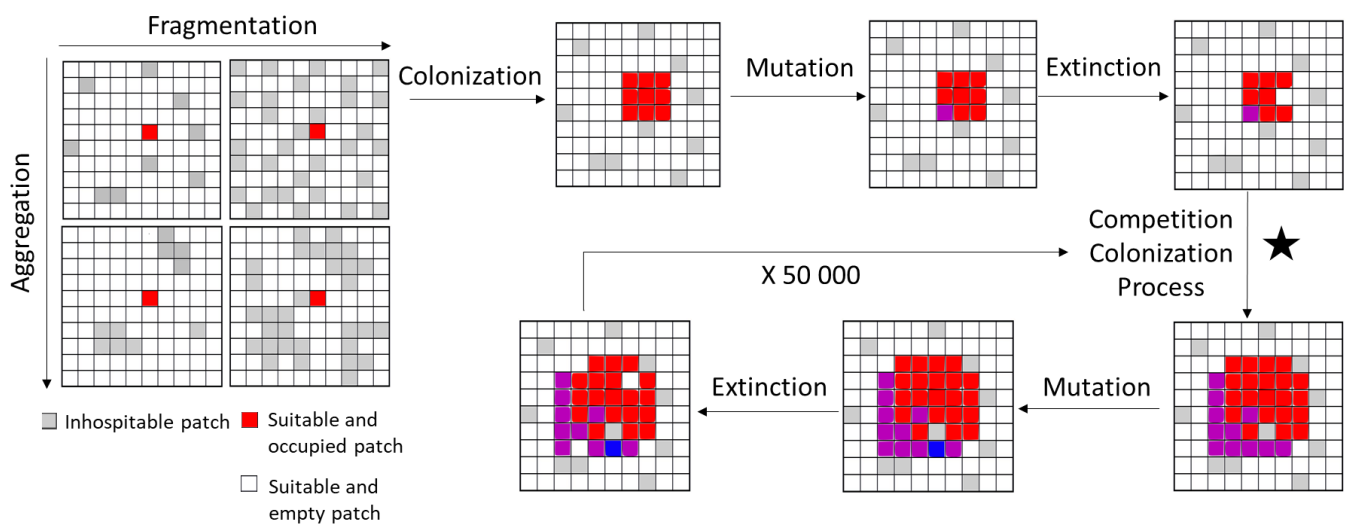
313 strongly depend on the trade-off structure associated with dispersal traits. Recent works stress  
 314 the importance of dispersal syndromes (Stevens et al. 2014, Raffard et al. 2022), i.e. the fact  
 315 that dispersal traits may be directly coupled to traits defining ecological interactions. The  
 316 competition/colonization trade-off falls within this category, as variations of dispersal are  
 317 directly coupled to competition hierarchies. Our results therefore illustrate how such a  
 318 syndrome could lead, for some landscapes, to the selection of higher dispersal, while works  
 319 that consider evolution of dispersal alone (e.g., Hastings, 1983; Travis & Dytham, 1999)  
 320 would produce the reverse pattern. Application of either framework of course depends on the  
 321 types of organisms that are considered and whether dispersal traits are competitively costly.

322 In particular, our model assumes that the fecundity of the organism under  
 323 consideration, i.e., the number of offspring produced, increases with increasing dispersal  
 324 distance. This provides an additional advantage for dispersive strategies that will produce  
 325 many more offspring and therefore occupy space more quickly if there is no superior  
 326 competitor present. Many previous models do not make this assumption and use constant  
 327 fecundity (eg, Bonte et al., 2010; Travis & Dytham, 1999). This hypothesis may influence our  
 328 results in several ways. With constant fecundity, selection of dispersive strategies is likely



329 reduced, leading to a smaller mean dispersal in highly fragmented habitats, lower abundances  
 330 in the landscape, and early extinctions. Dispersal polymorphism should stay present because  
 331 isolated patches can only be reached by dispersive strategies. However, this assumption of  
 332 increasing fecundity with increasing dispersal distance is not biologically irrelevant and can  
 333 be linked to various groups of organisms. A certain amount of energy could be allocated in  
 334 either a few large, poorly dispersing offspring or in many small, highly dispersing offspring.  
 335 This rationale has been largely used in the context of variations of plant seed size (eg, Henery  
 336 & Westoby, 2001; Muller-Landau et al., 2008). It could also apply in the context of social  
 337 insect colonies. For instance, in ants with the production of large propagules consisting of a  
 338 queen and workers that disperse over short distances or small propagules of a single queens  
 339 dispersing over long distances (Cronin et al. 2013).

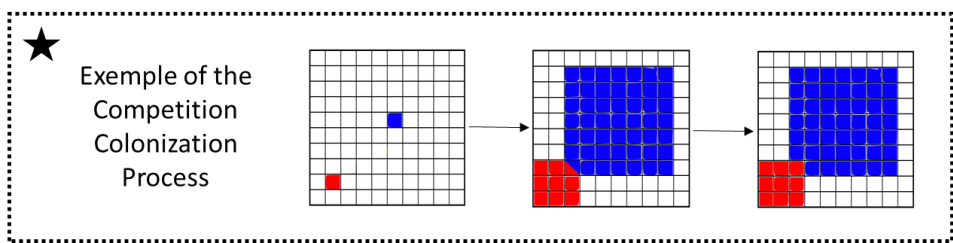
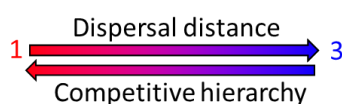
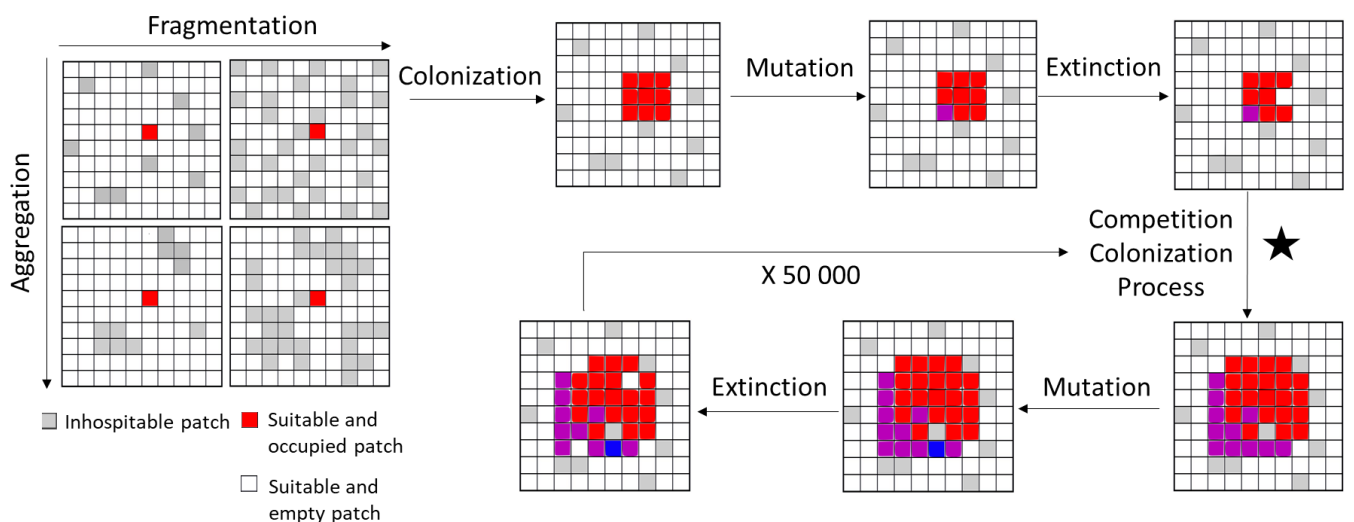
340 We explain the selection of higher dispersal in fragmented landscapes by two  
 341 mechanisms. First, fragmentation decreases overall occupancy (on the entire grid). Thereby,  
 342 when a patch is emptied, the number of possible colonizers (ie, of suitable filled patches) is  
 343 reduced. This reduces the average competition level. The advantage of competitive strategies  
 344 is therefore reduced. Second, fragmentation intensifies the strength of the competition for



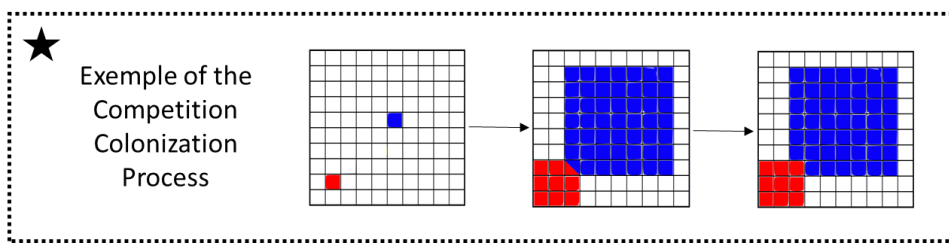
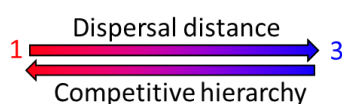
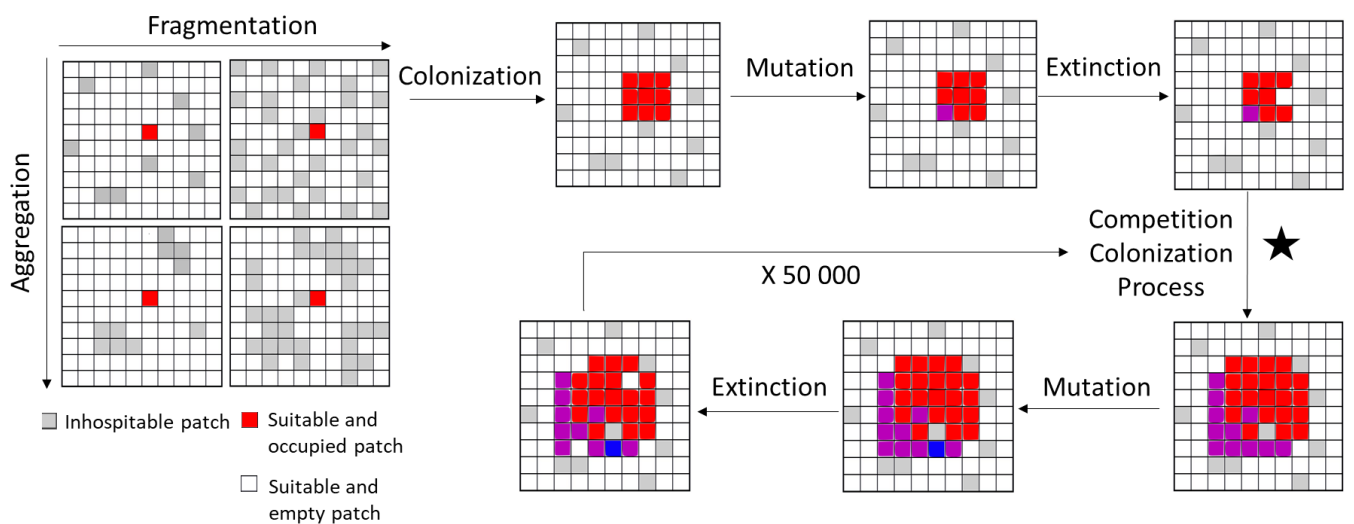


345 space which favors colonizers. Isolated patches in fragmented landscapes can only be  
 346 exploited by highly dispersive strategies. Effects of fragmentation on mean levels of dispersal  
 347 have led to contrasted results in empirical studies (Cheptou et al. 2017). Our results of a  
 348 selection of higher dispersal is for instance coherent with empirical studies of nuthatches  
 349 (*Sitta europaea*) in Belgium (Matthysen et al. 1995). Similarly, metapopulation study of the  
 350 Glanville fritillary in Finland shows that isolated patches of the metapopulation act as positive  
 351 filters for the more dispersive strategies (Hanski et al. 2004) and that this variation can be  
 352 linked to allelic variations constraining flight metabolism (Haag et al. 2005). Conversely, a  
 353 decrease of dispersal at higher fragmentation levels has been observed in various animal or  
 354 plant species (Schtickzelle et al. 2006, Bonte et al. 2006, Cheptou et al. 2008). Spatial  
 355 heterogeneity and competition decrease are two forces that act with opposite effects, the  
 356 former decreasing dispersal (higher dispersal cost) while the latter increases it (decreased  
 357 abundancies in fragmented landscapes, relax competition). The importance of each force  
 358 varies among species and needs to be systematically considered to better predict changes in  
 359 dispersal.

360 We found that aggregation largely reduces the selection of dispersal strategies, to the



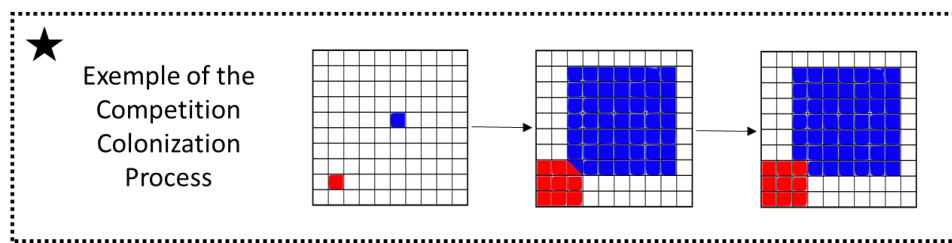
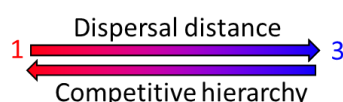
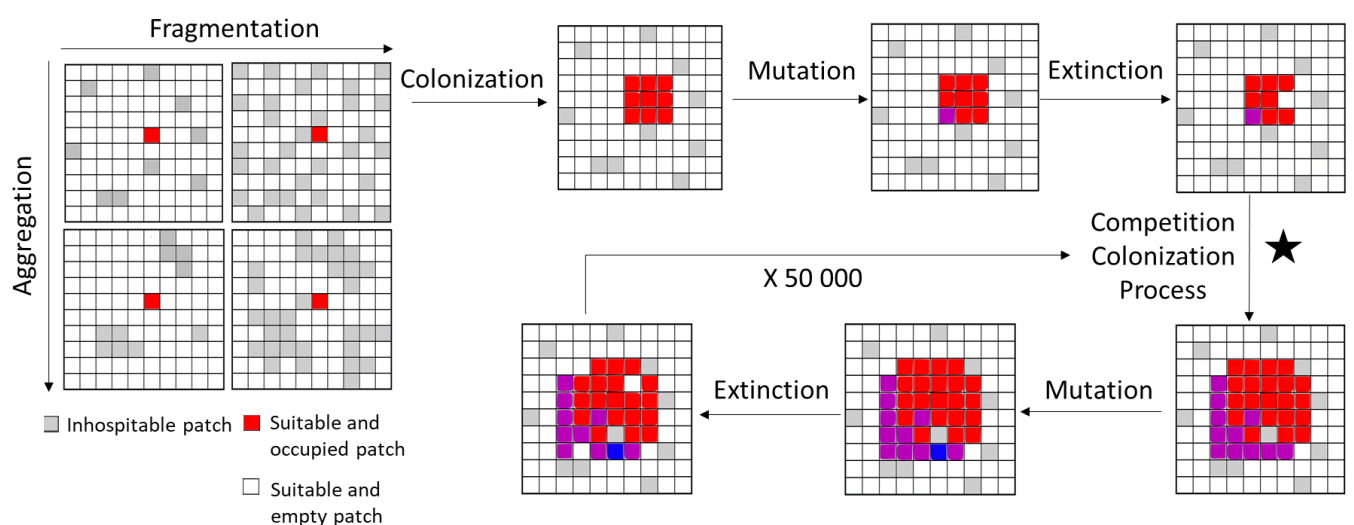
361 extent that such a selection cannot even be detected when aggregation is larger than 40%.  
 362 This points out the importance of spatially explicit models. In a previous work, Hiebeler  
 363 (2000) showed how mean field approximations provide accurate occupancy predictions for  
 364 random fragmented landscapes, but not when aggregation exists. Similarly, we show here that  
 365 while our results on dispersal evolution in random landscapes are coherent with mean field  
 366 approximations (Tilman et al. 1994), such approximations do not provide qualitatively  
 367 adequate variations when aggregation takes place. We explain the reduction of dispersal due  
 368 to aggregation by the fact that it favors the replacement of colonizers by competitors because  
 369 of a high probability to find a favorable patch next to another favorable patch. The landscape  
 370 is there continuous, so that competition is selected in such localities. Such a result is in line  
 371 with Bonte et al. (2010) who found an increase of local dispersal (our competitive strategy)  
 372 and a decrease of long-distance dispersal (our colonizer strategy) in aggregated fragmentation  
 373 scenarios. Note that our aggregated, fragmented scenarios also yield landscapes in  
 374 which connectivity among patches largely varies. While such variations could favor dispersal  
 375 by fostering spatial variance in the competition context (Henriques-Silva et al. 2015) or yield  
 376 dispersive strategies in large patches (Gros et al. 2006), accounting for a competition-  
 377 colonization trade-off here yields the opposite result. Again, a precise assessment of costs



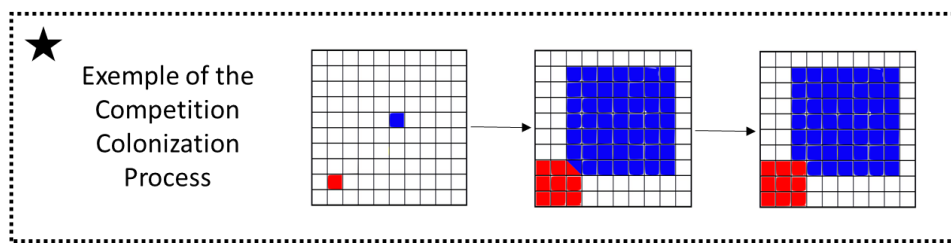
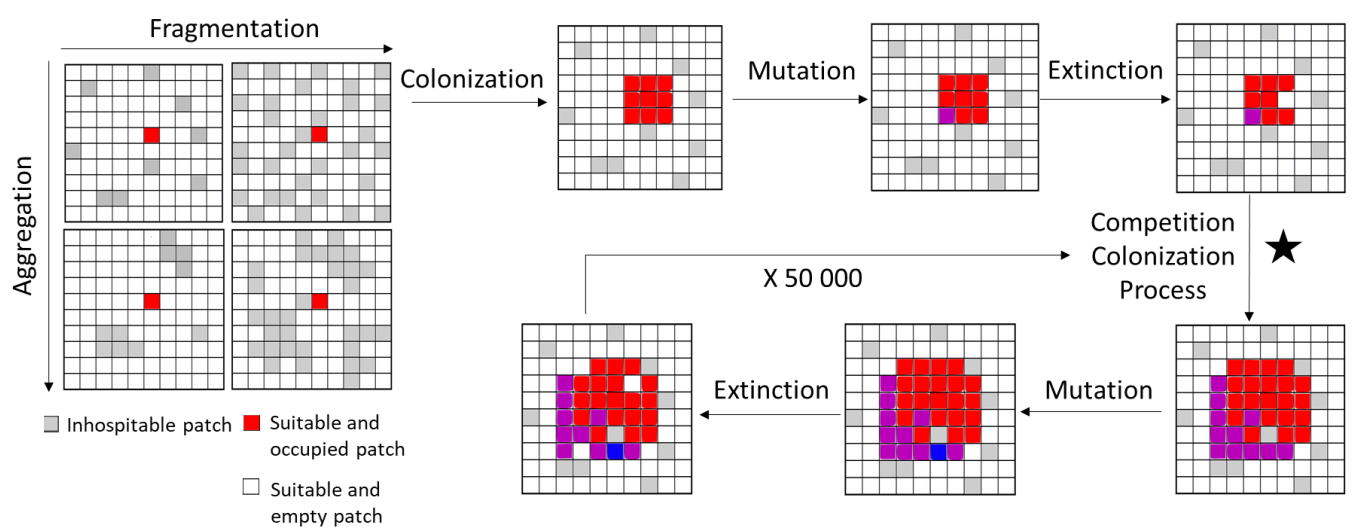
378 associated with dispersal will therefore be key to understanding potential outcomes. All these  
 379 studies however underline the necessity of spatially explicit approaches to better understand  
 380 the dynamics of fragmented metapopulations (Hiebeler 2000, Henriques-Silva et al. 2015).  
 381 Here, a simple mean-field approach would yield an overestimation of dispersal evolution and  
 382 of associated evolutionary rescue effects.

383 Our model is based on mutations and on the selection of certain phenotypes resulting  
 384 from these mutations. While our results can be largely interpreted from a selection point of  
 385 view, we explicitly account for stochastic components, both in the mutation process and in the  
 386 random patch extinction process. This latter source of stochasticity leads to genetic drift in  
 387 our simulations. Effects of drift are particularly visible for small metapopulation sizes (ie, on  
 388 the brink of extinction), and indeed we observed broader distributions of phenotypic values in  
 389 such conditions. To assess the importance of these stochastic components, we undertook 20  
 390 replications of each parameter combination in scenario one and 40 in scenario two. The  
 391 consistent qualitative variations of dispersal distances however suggest a large role of  
 392 selective processes.

393 We observe dispersal polymorphism when fragmentation is high and aggregation low

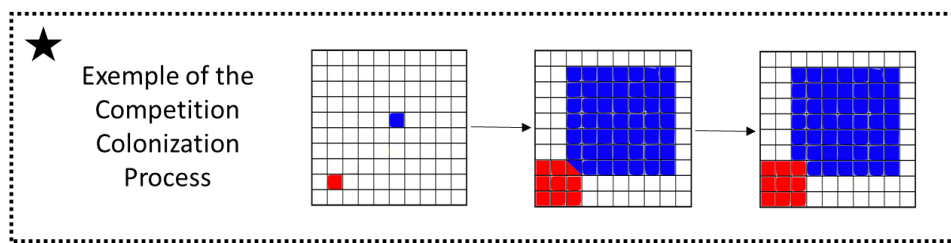
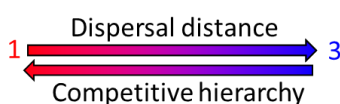
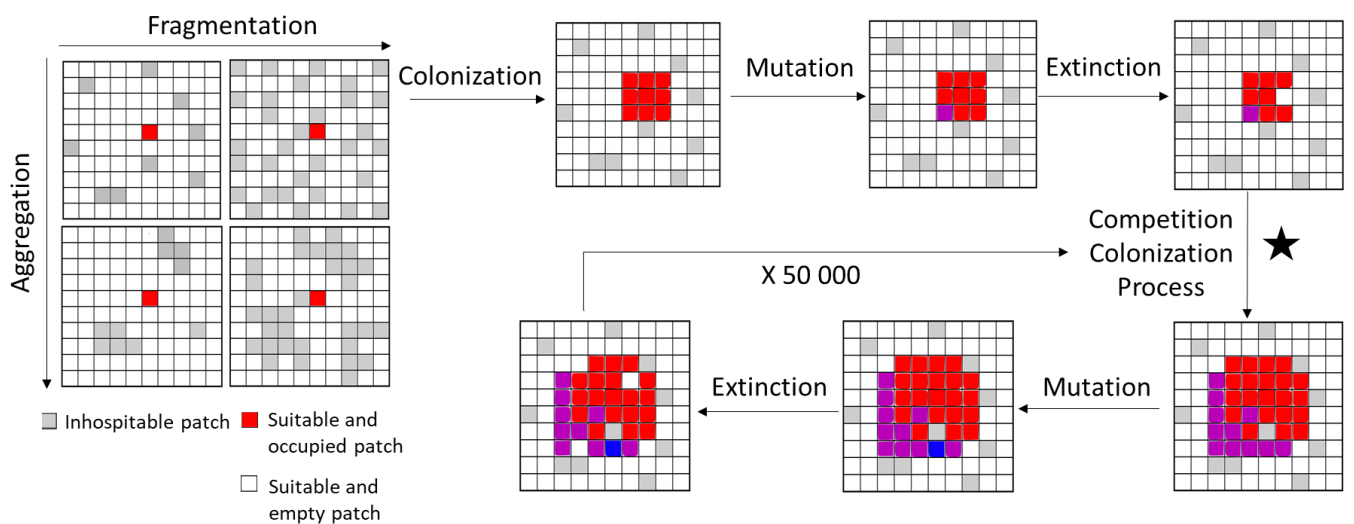


394 to intermediate. Such landscapes contain a mix of large aggregates of patches and of isolated  
 395 patches. The strategy favored in the aggregates of patches is more competitive, and the  
 396 dispersal distance selected there depends on how loose the aggregates are. When aggregation  
 397 produces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

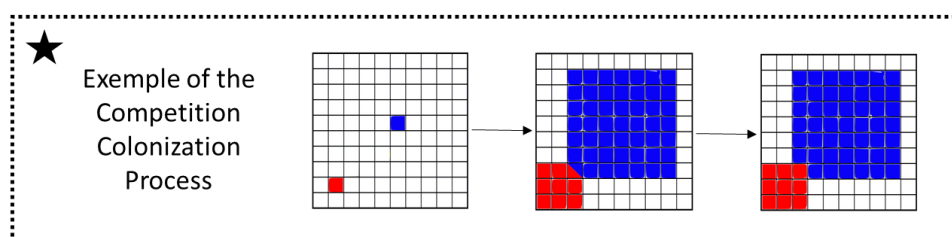
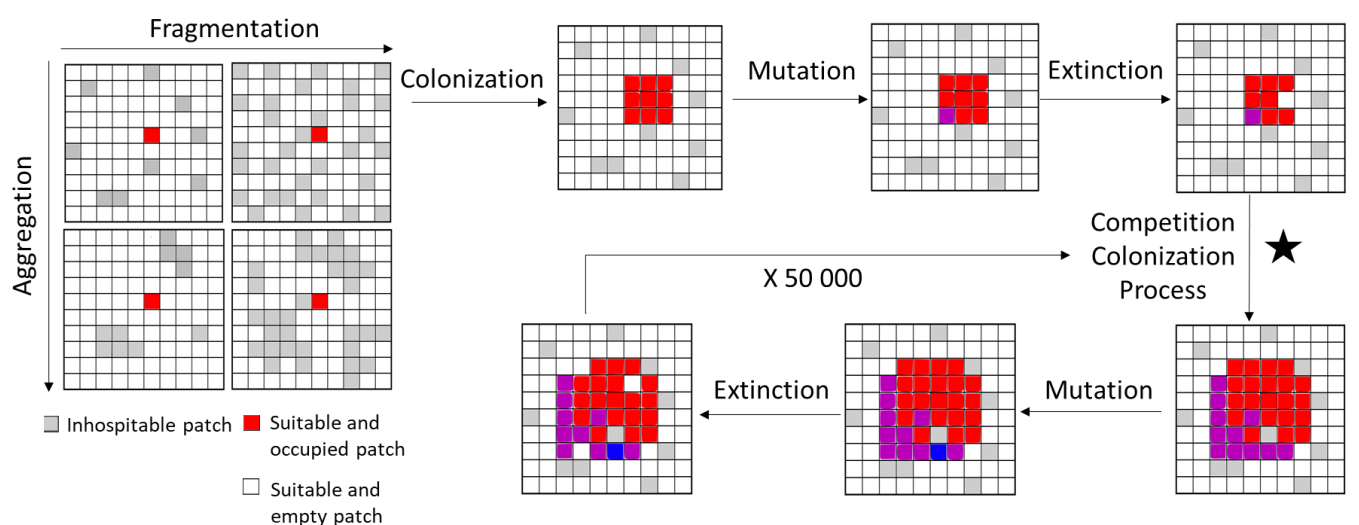


411 evolutionary rescue.

412 Evolutionary rescue can be construed as a race between speed of adaptation and of  
413 environmental deterioration. Hence, the faster the evolution and the slower the perturbation,  
414 the more likely the rescue. We observe that such expectations are met when fragmentation is  
415 random (no aggregation). Dispersal evolution delays the extinction of the population when  
416 fragmentation rate is low and mutation rate high. Fast selection of good dispersers then  
417 occurs. As these are adapted to occupy isolated patches, such strategies foster spatial rescue in  
418 the highly fragmented landscapes. Slow evolution would not allow that. At the onset of  
419 fragmentation, the grid is continuous, and mostly occupied by competitors. If fragmentation is  
420 too fast, there is no time for dispersers to appear and become selected and to fill isolated  
421 patches. Interestingly, our study shows that rescue happens as a jump phenomenon, being  
422 only possible when mutation rates are higher (10 times higher in our model) than perturbation  
423 rates. No evolutionary rescue occurs when fragmentation is aggregated. Aggregation delays  
424 extinction by itself even without evolution. Under high fragmentation and aggregation levels,  
425 suitable patches make small continuous groups that facilitate the local persistence of  
426 competitors. In an aggregated context, dispersal evolution is absent or strongly constrained

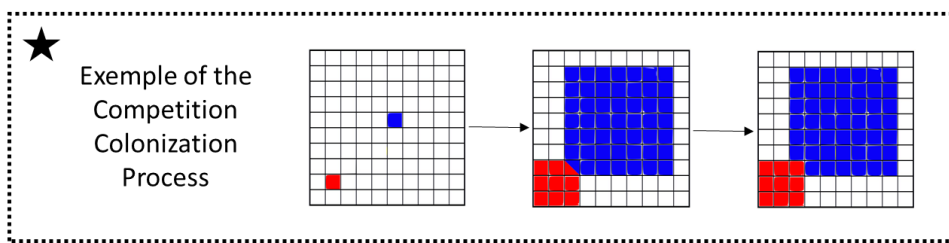
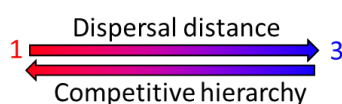
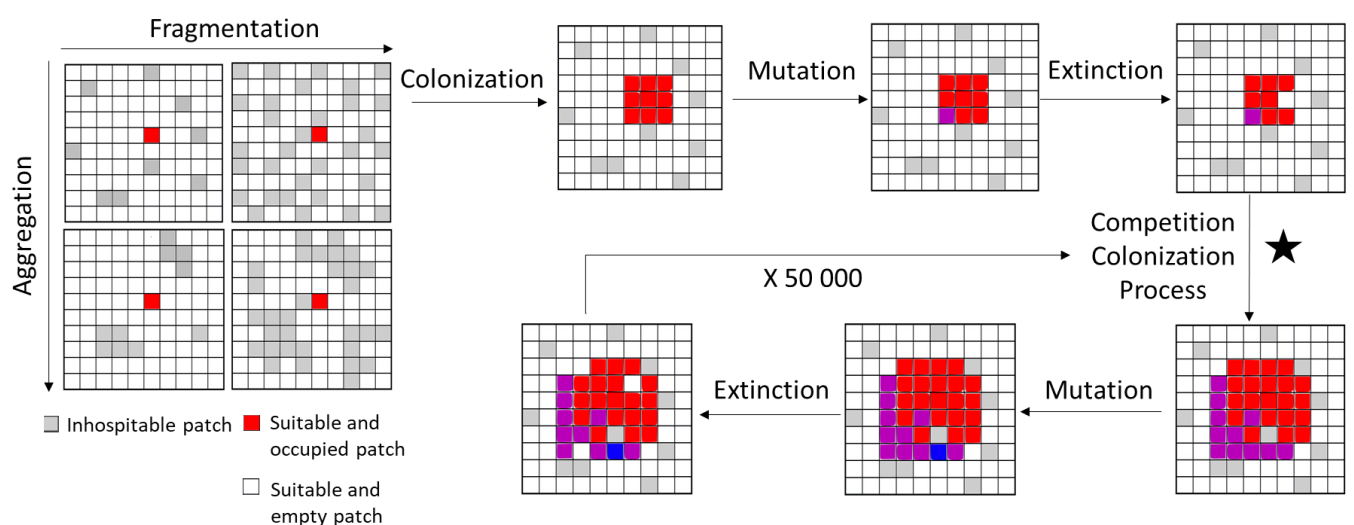


427 (blue curves on Fig. 2a) so that little evolutionary potential exists. In the absence of such an  
 428 adaptive potential, evolutionary rescue cannot act. Our results on the possibility of rescue  
 429 through evolutionary changes of dispersal agree with former theoretical works where  
 430 fragmentation either stemmed from climatic changes (Boeye et al. 2012) or from  
 431 heterogeneities in mortality (Heino and Hanski 2001). While in the actual context of fast  
 432 environmental changes, it may seem complicated for species to evolve quickly enough (10  
 433 times faster than the perturbation), several examples of fast evolution of dispersal in  
 434 fragmented systems have been reported (reviewed in Cheptou et al., 2017). Whether such  
 435 evolution are sufficient to affect long term metapopulation persistence is however unknown.  
 436 The fact that evolutionary rescue does not happen here in aggregated landscapes also has  
 437 important implications. The current fragmentation of habitats is a complex non-random  
 438 process that may be frequently auto-correlated in space, therefore producing aggregated  
 439 structures. For instance, the construction of additional urban areas next to existing urban areas  
 440 creates aggregated landscapes. Studies from the Tabriz Metropolitan Area (Iran) show that the  
 441 destruction of suitable habitats surrounding the cities result in the creation of aggregated non-  
 442 suitable patches (Dadashpoor et al. 2019a, b). Aggregation of fragmentation can also be  
 443 linked to the displacement and development of agricultural activities. In Beijing City, China,



444 landscape patterns show important and complicated changes in the distribution of urban and  
 445 agricultural lands. Economic development expands cultivated land and construction into  
 446 forests and grasslands resulting in aggregated and less diverse landscapes (Li et al. 2017). We  
 447 propose that when fragmentation happens in such aggregated ways, evolution will likely play  
 448 a minor role in the maintenance of the metapopulation.

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



460

461 **FUNDING**

462 Basile Finand was funded by the ministry of higher education.

463 **DATA AVAILABILITY**

464 Model and analysis scripts are available on github:

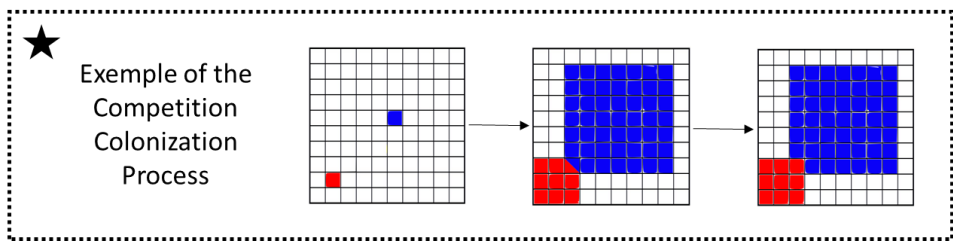
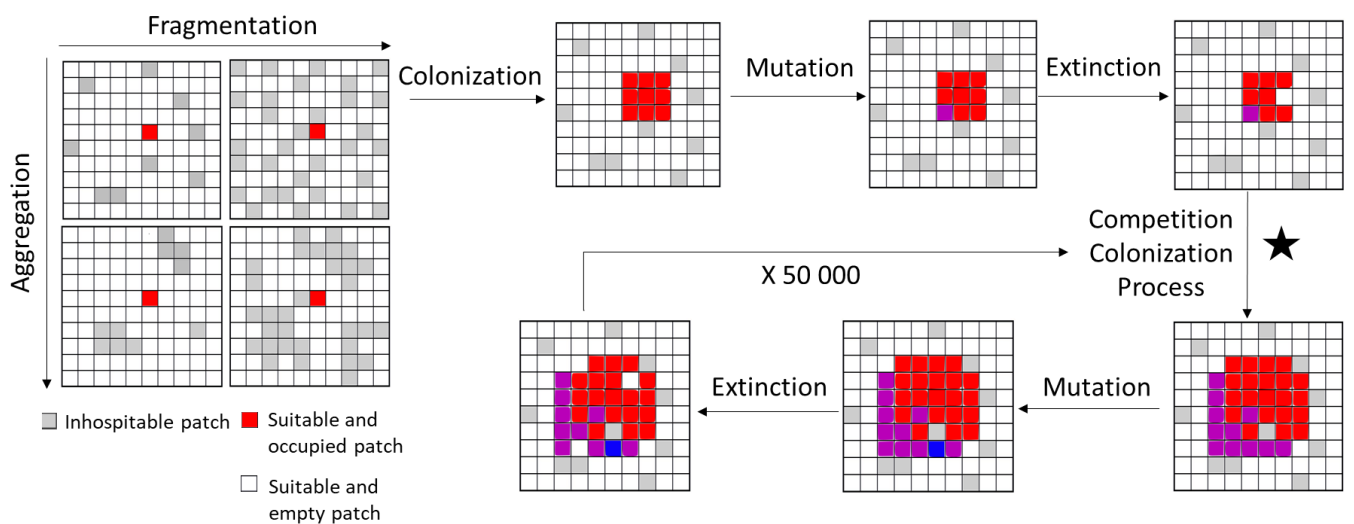
465 [https://github.com/bfinand/Model\\_dispersal\\_evolution](https://github.com/bfinand/Model_dispersal_evolution)

466 **CONFLICT OF INTEREST**

467 The authors declare no conflict of interest.

468 **ACKNOWLEDGMENT**

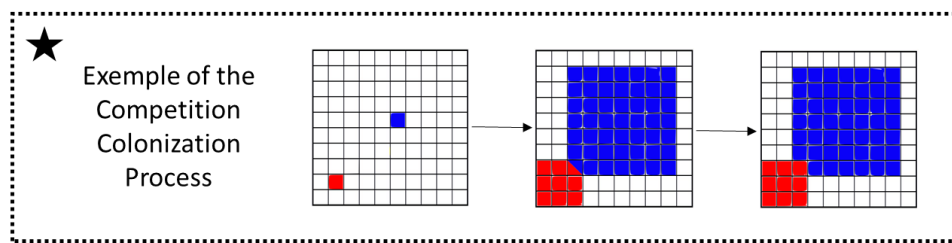
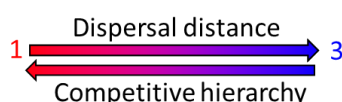
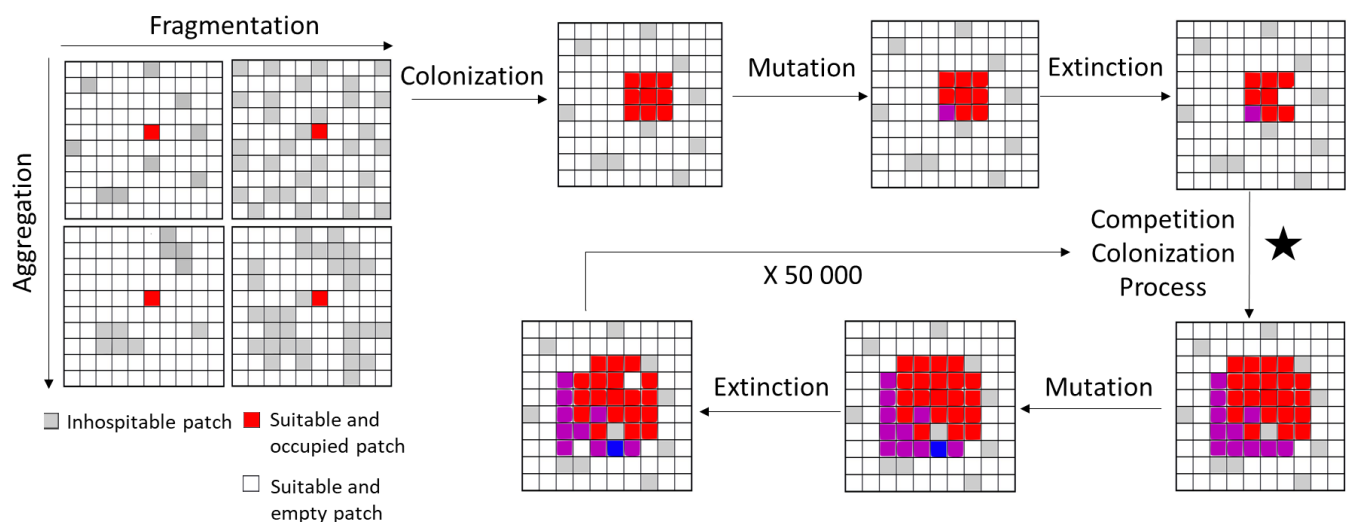
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471 (<https://doi.org/10.24072/pci.ecology.100426>).





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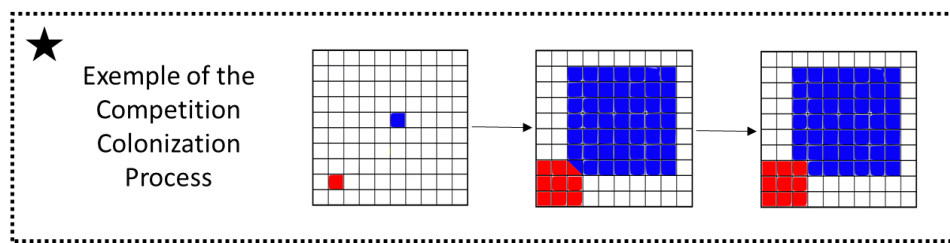
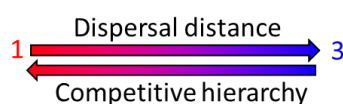
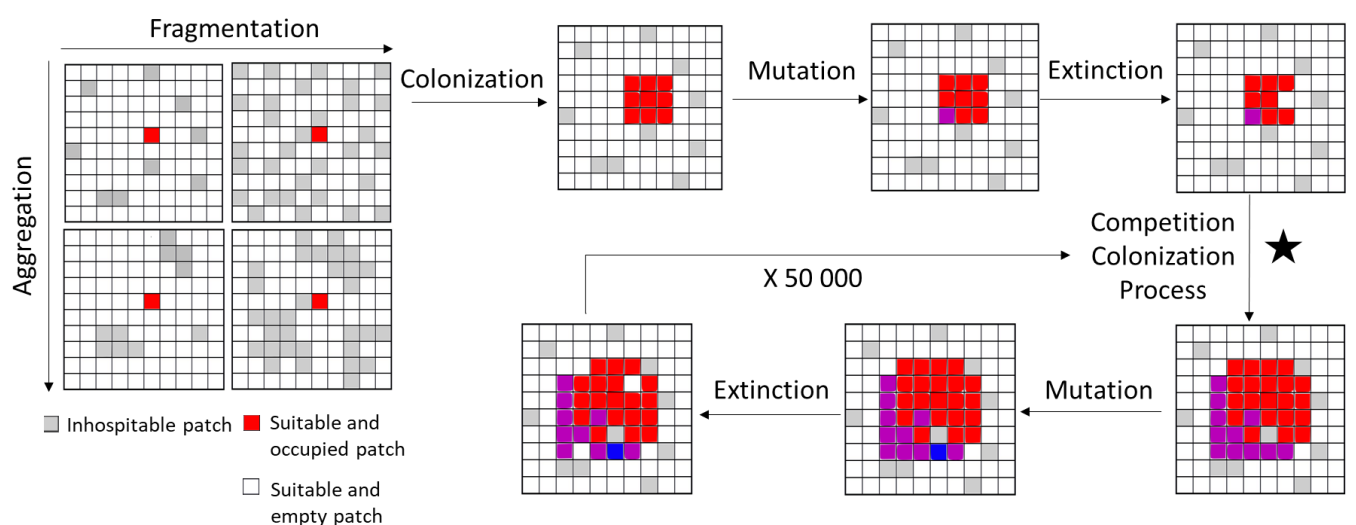
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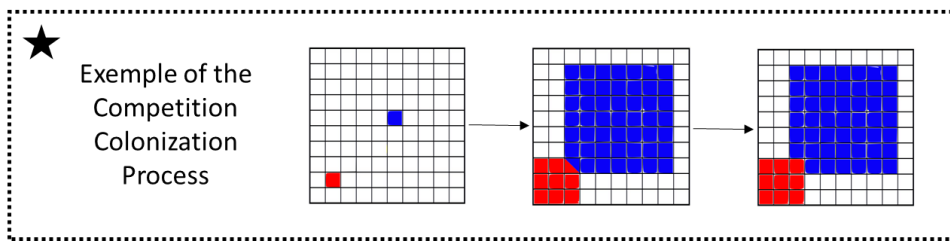
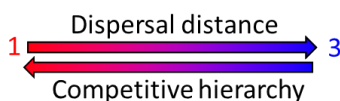
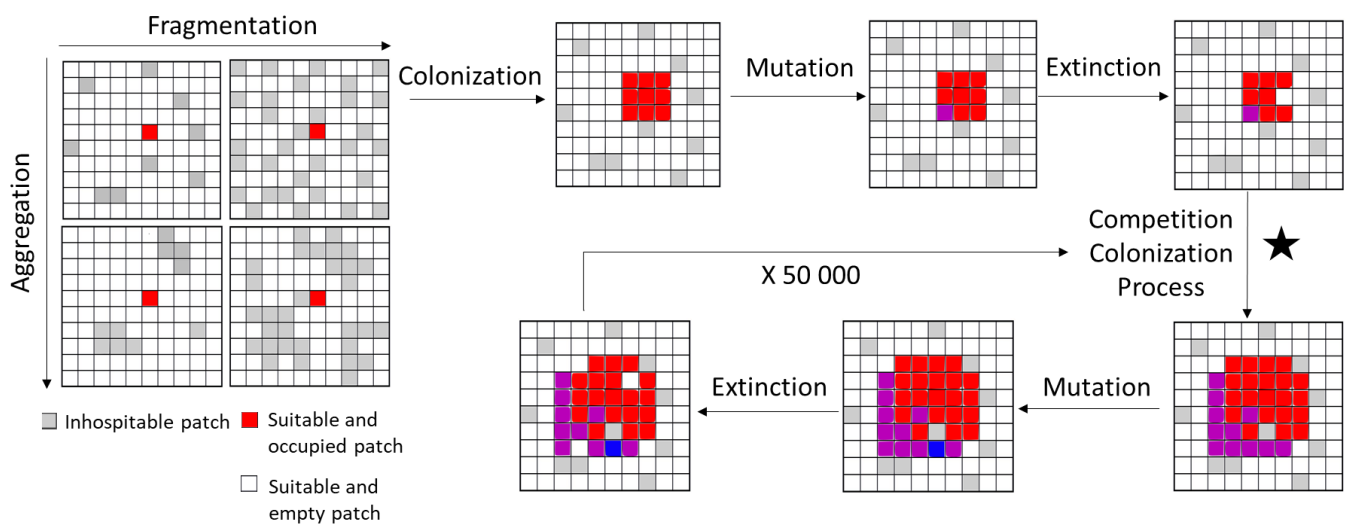
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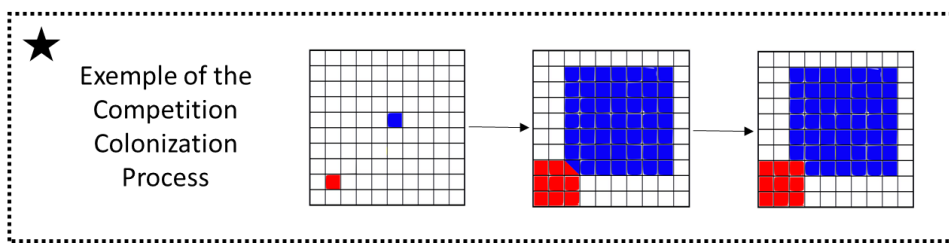
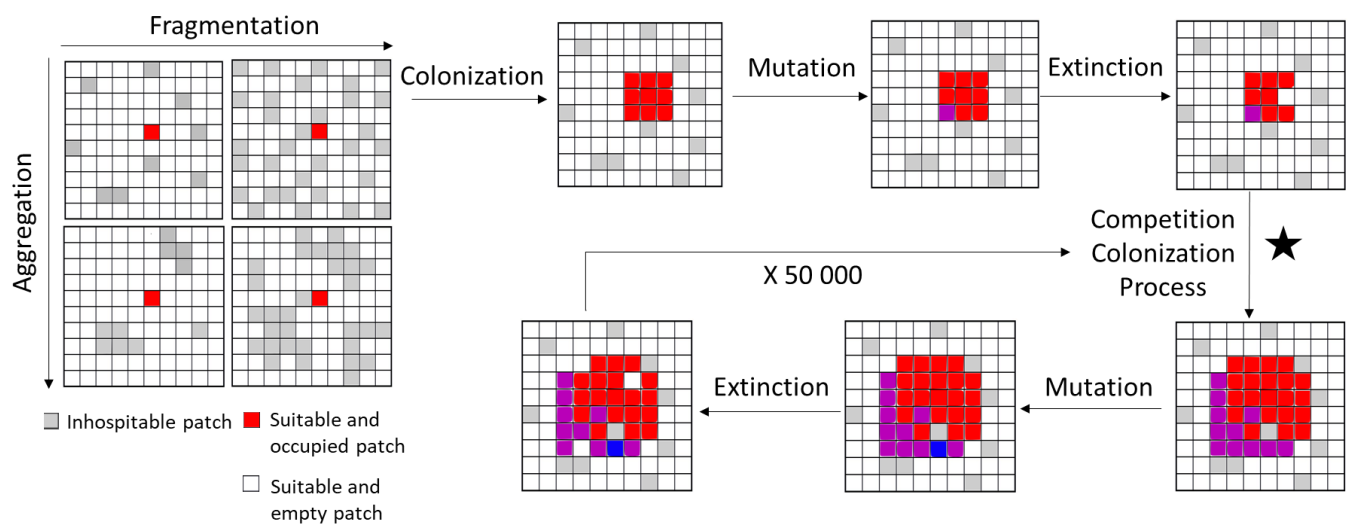
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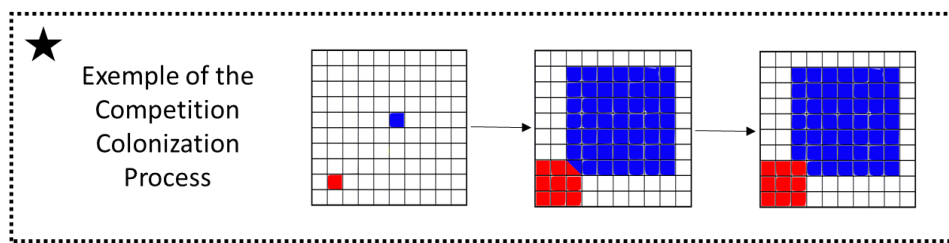
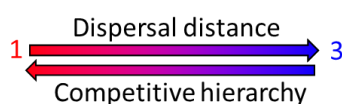
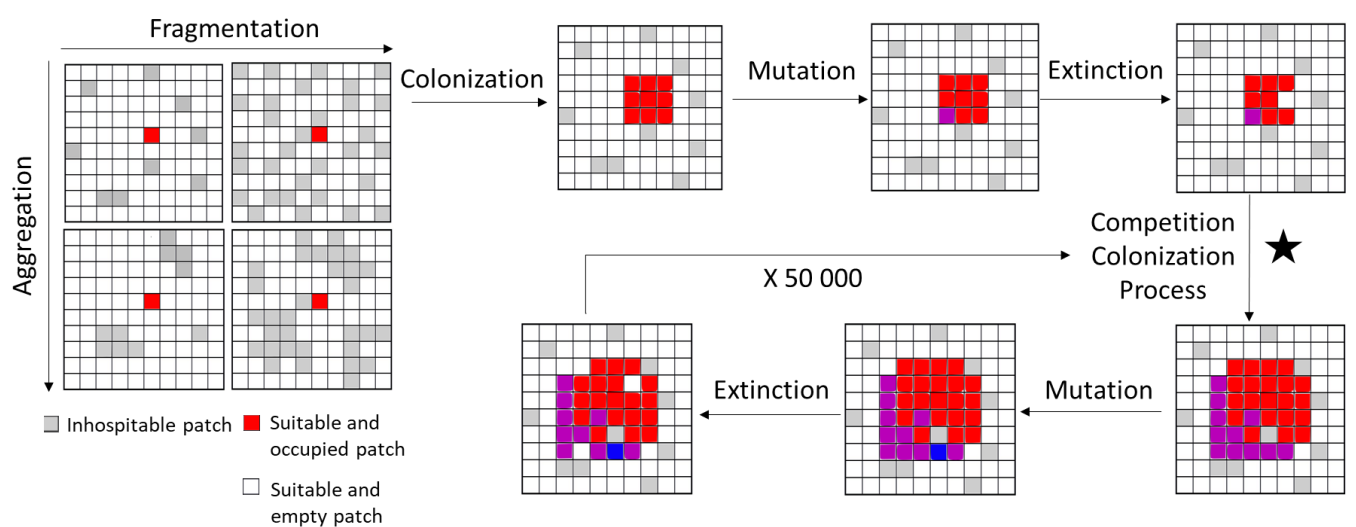
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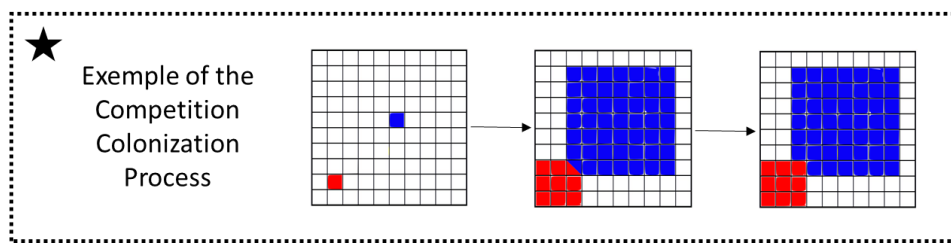
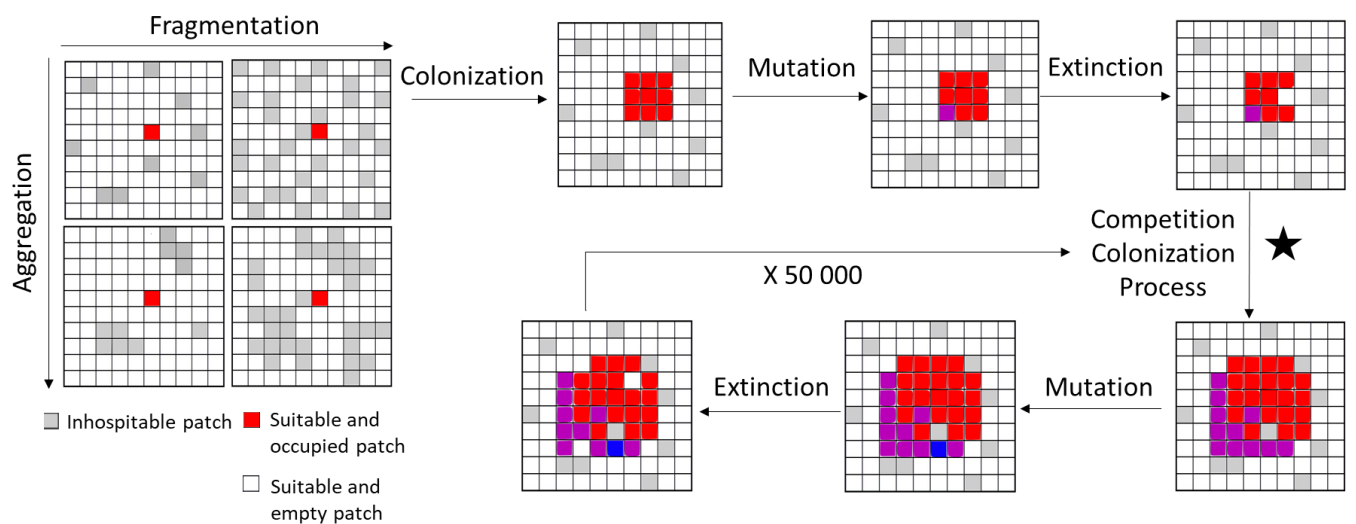
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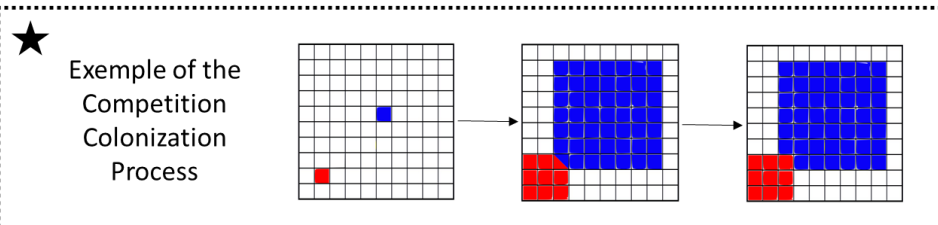
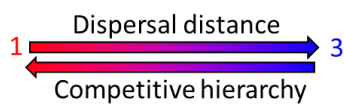
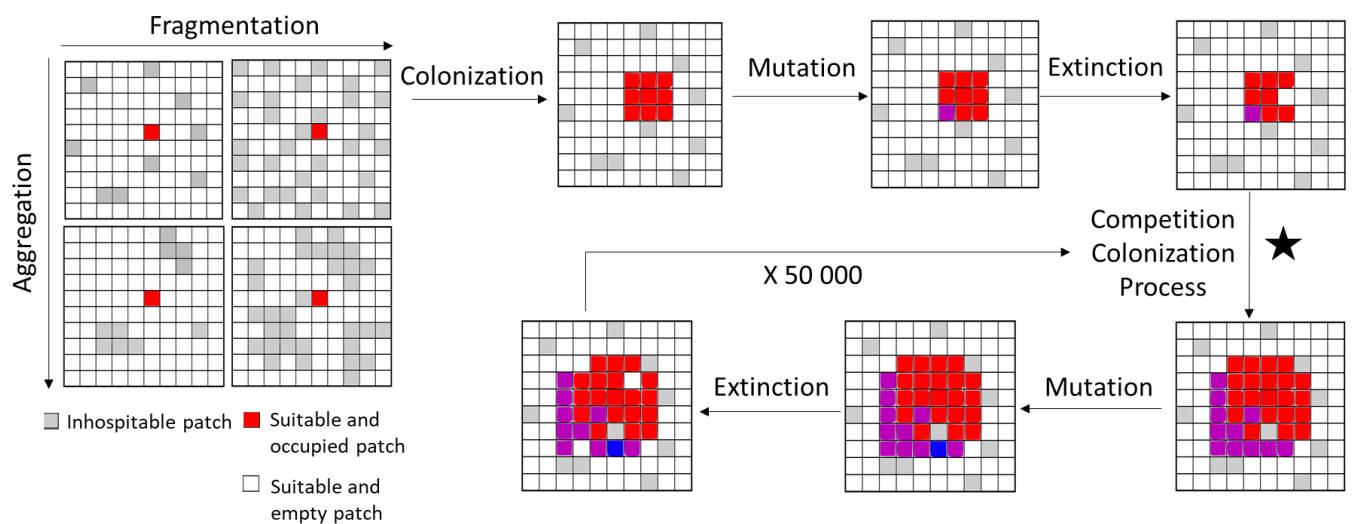
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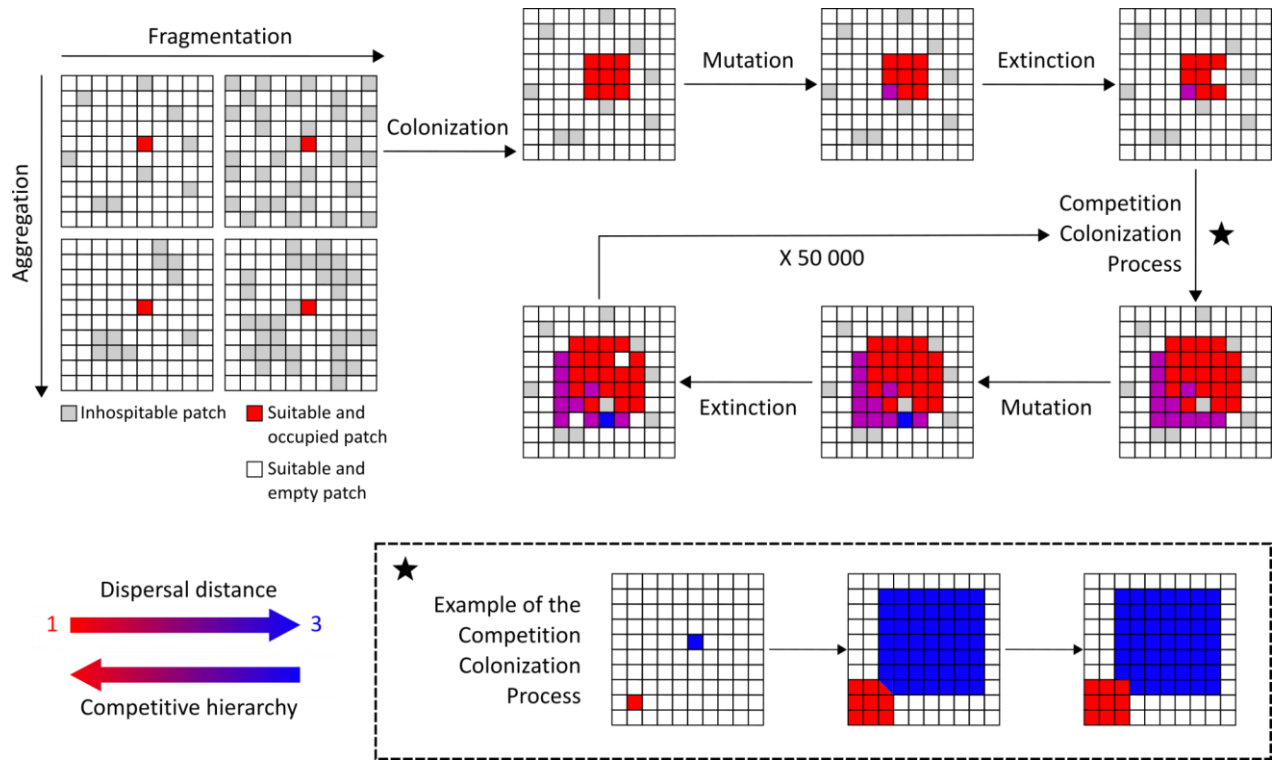
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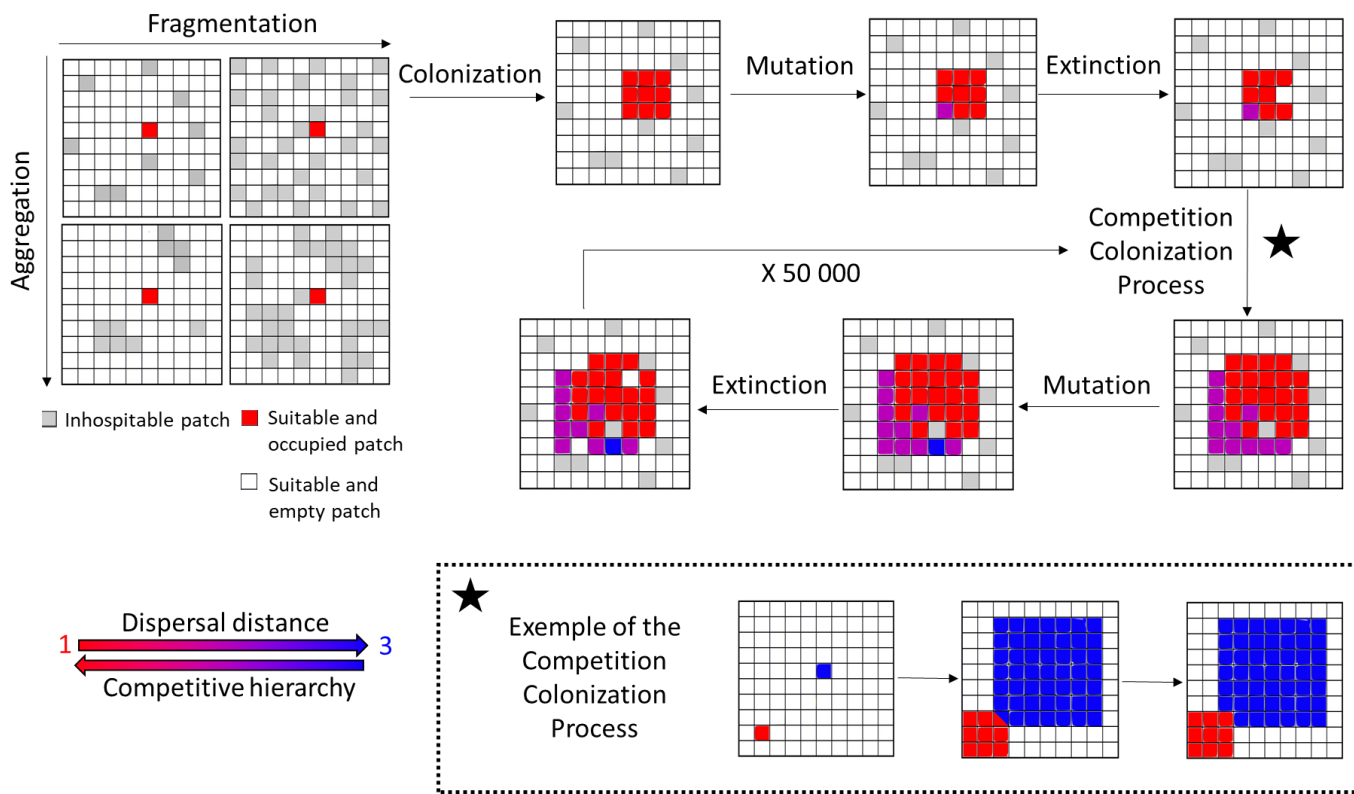






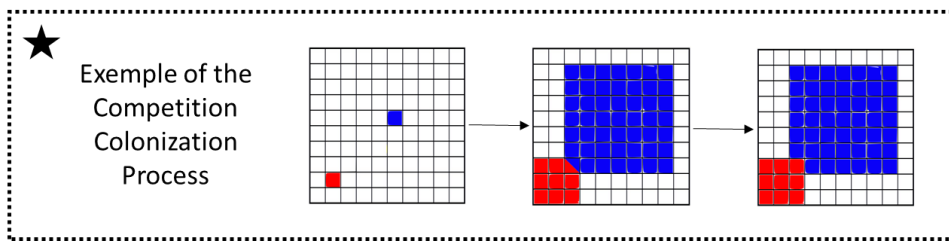
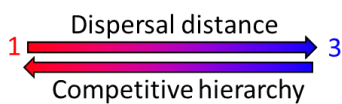
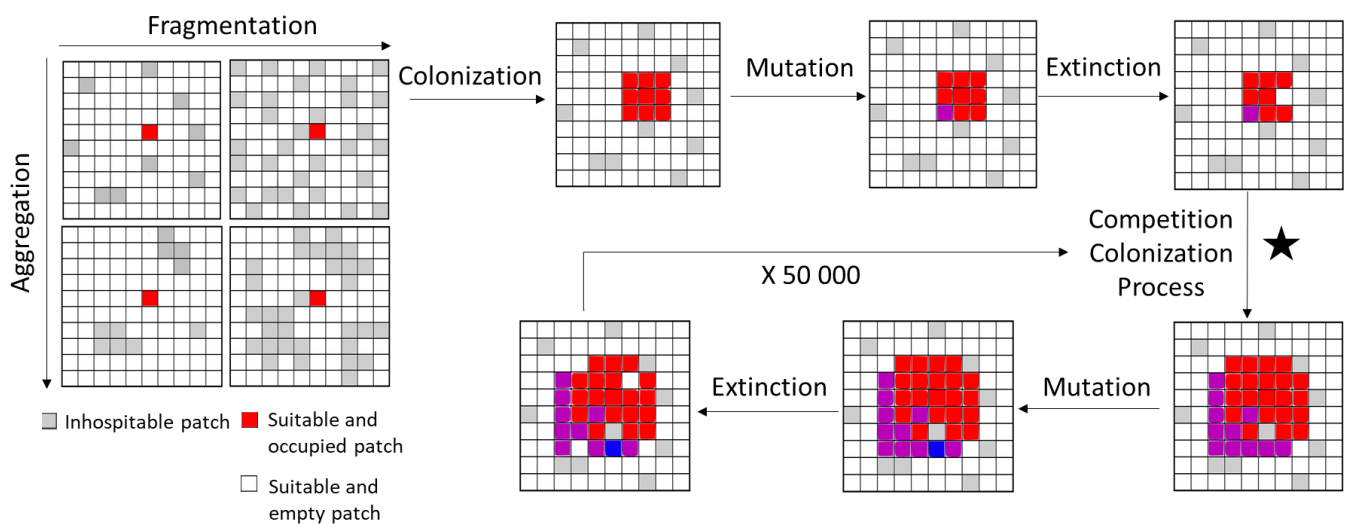
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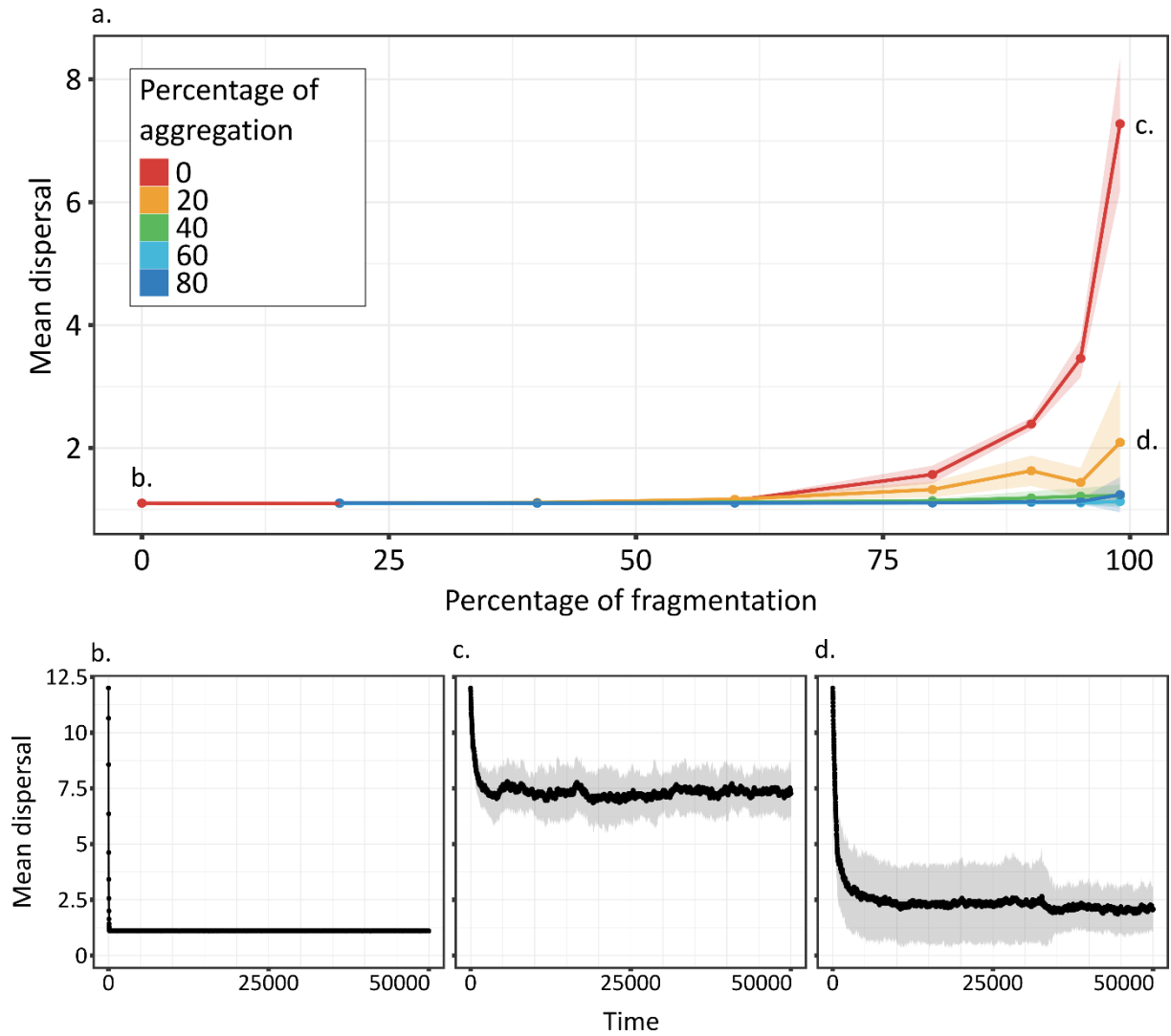
599 **Figure 1:** Illustration of a simulation based on the competition/colonization tradeoff in a fixed  
 600 environment scenario. Upper panels detail the various parts of a given timestep, while the box  
 601 below shows the competition/colonization process when two individuals arrive on the same  
 602 patch. For each time-step, individuals colonize all suitable and empty patches within their



603 dispersal distance. Individuals mutate with a small probability. If a mutation occurs, the  
 604 dispersal distance of the individual is modified by 1, upward or downward with equal  
 605 probability. Extinction events follow, with a probability  $e$ . If two (or more) individuals arrive  
 606 on the same patch, the one with the smallest dispersal distance, being competitively dominant,  
 607 wins the patch. One simulation lasts 50 000 time-steps.

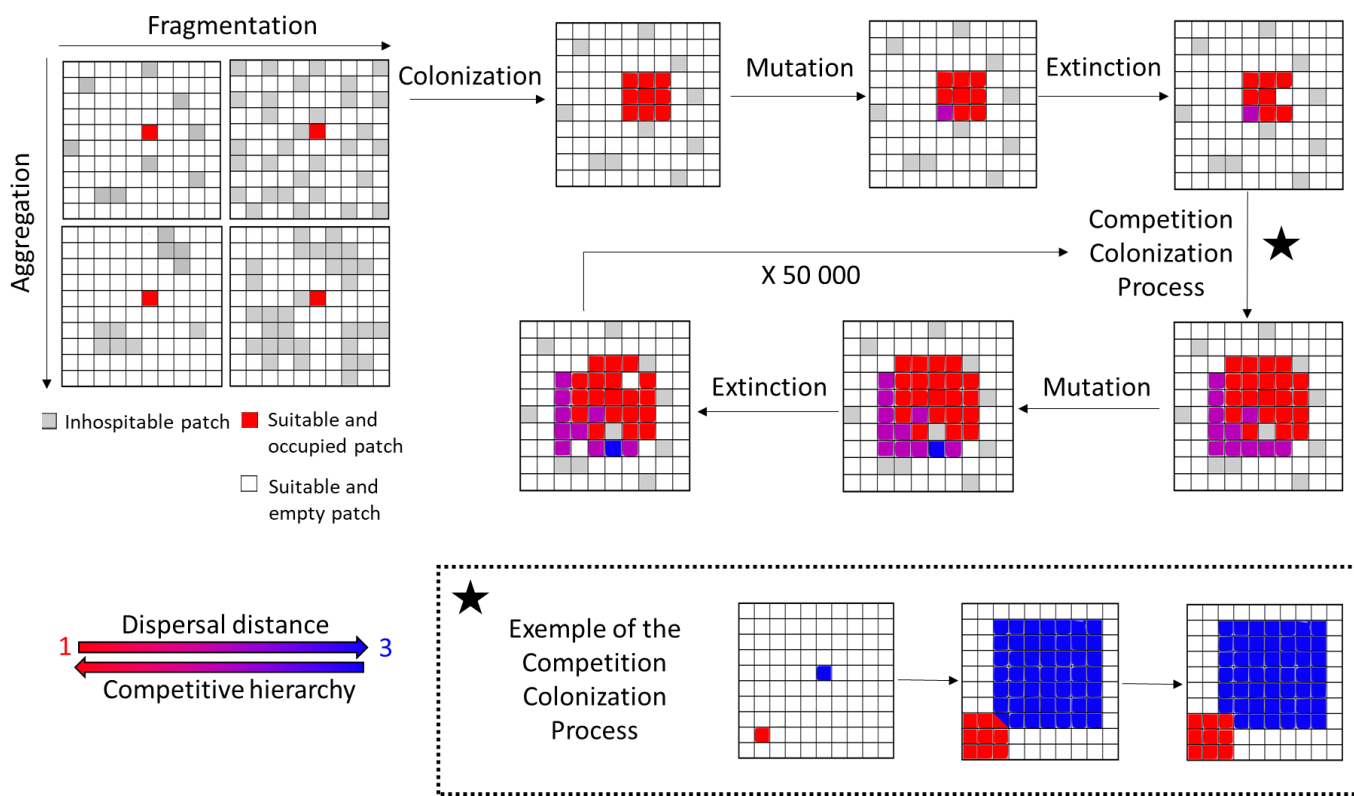
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610 **Figure 2:** Dispersal (mean +/- SD) at the end of simulations (at equilibrium) depending on

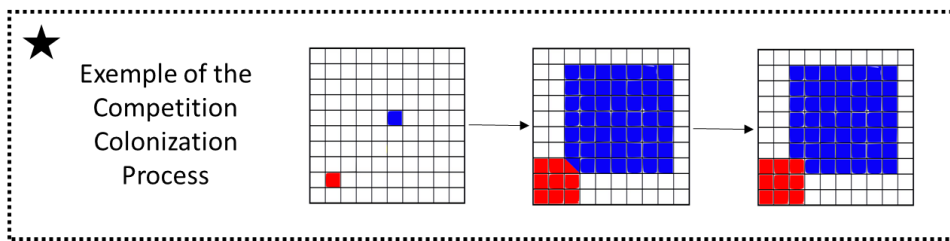
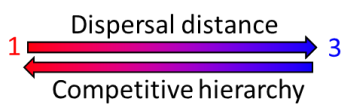
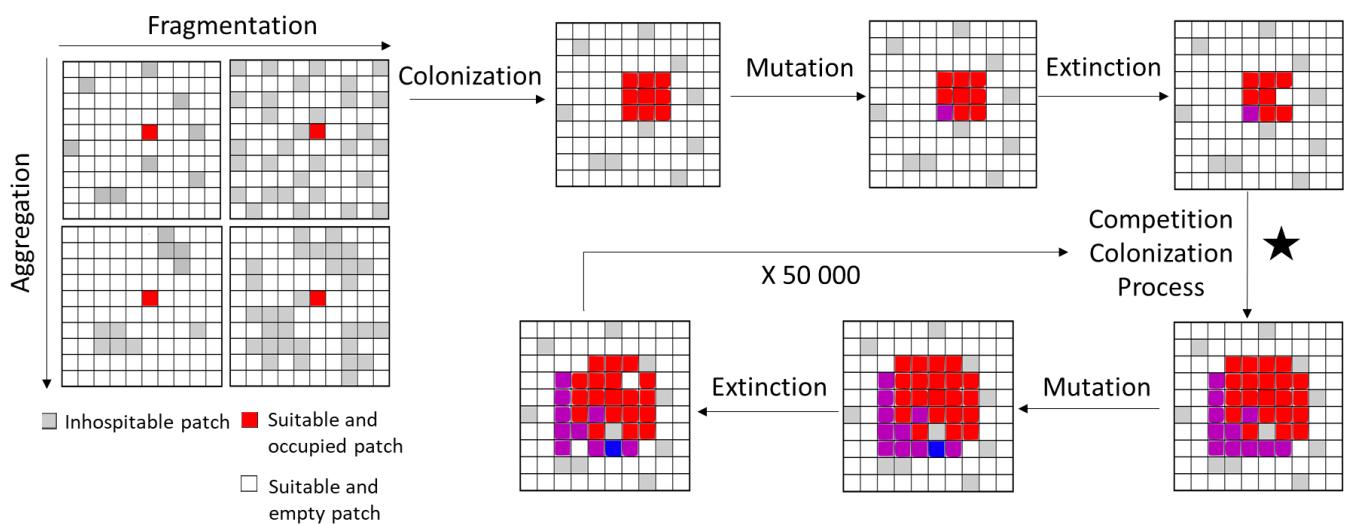


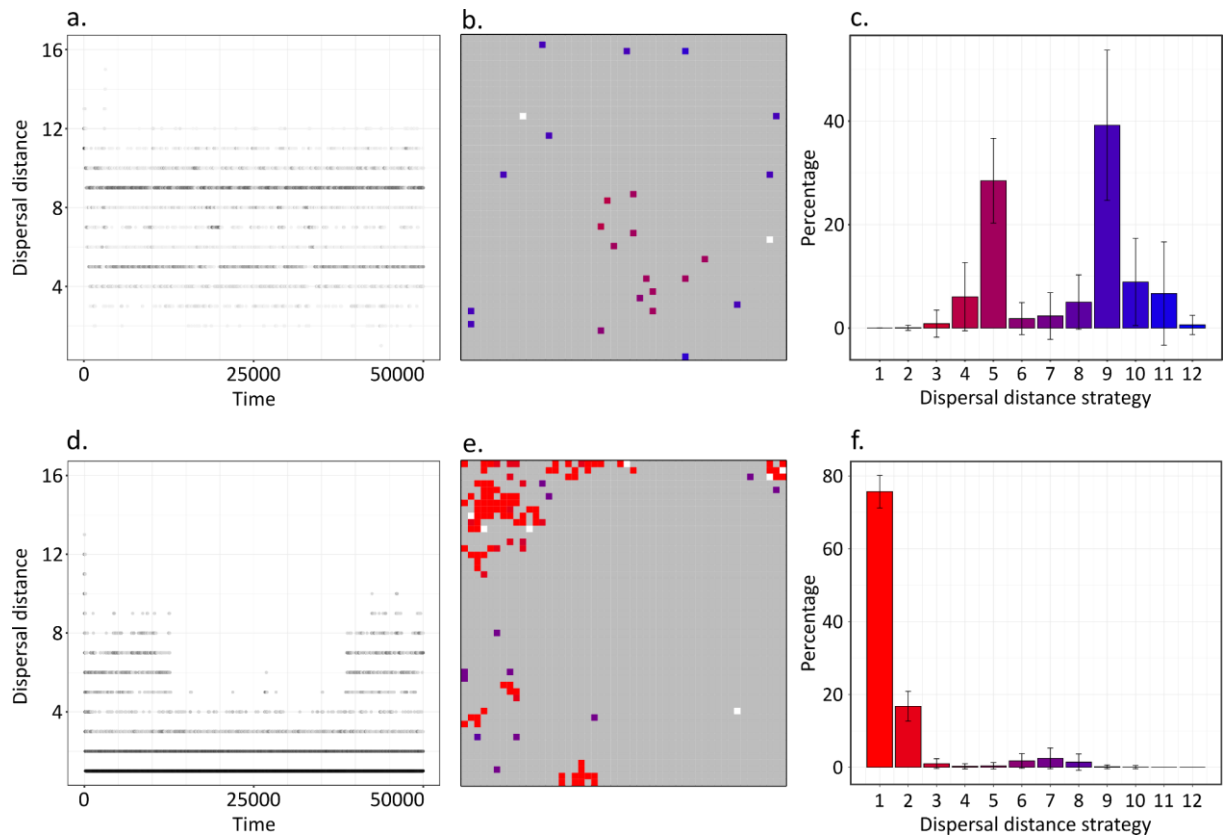
611 environment fragmentation and aggregation (a), and over time (b-d) for the 20 replicates for  
 612 conditions of no fragmentation and no aggregation (b), 99% of fragmentation and no  
 613 aggregation (c) or 99% of fragmentation and 20% of aggregation (d). Note that higher  
 614 dispersal distance is selected in random fragmented landscapes, but that aggregation of  
 615 fragmentation lowers this selective effect. Shadows around curves represent SD.

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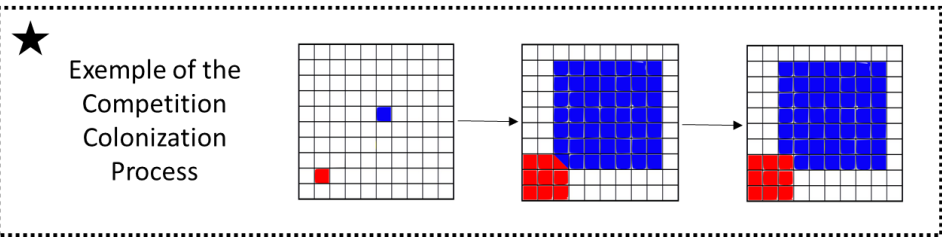
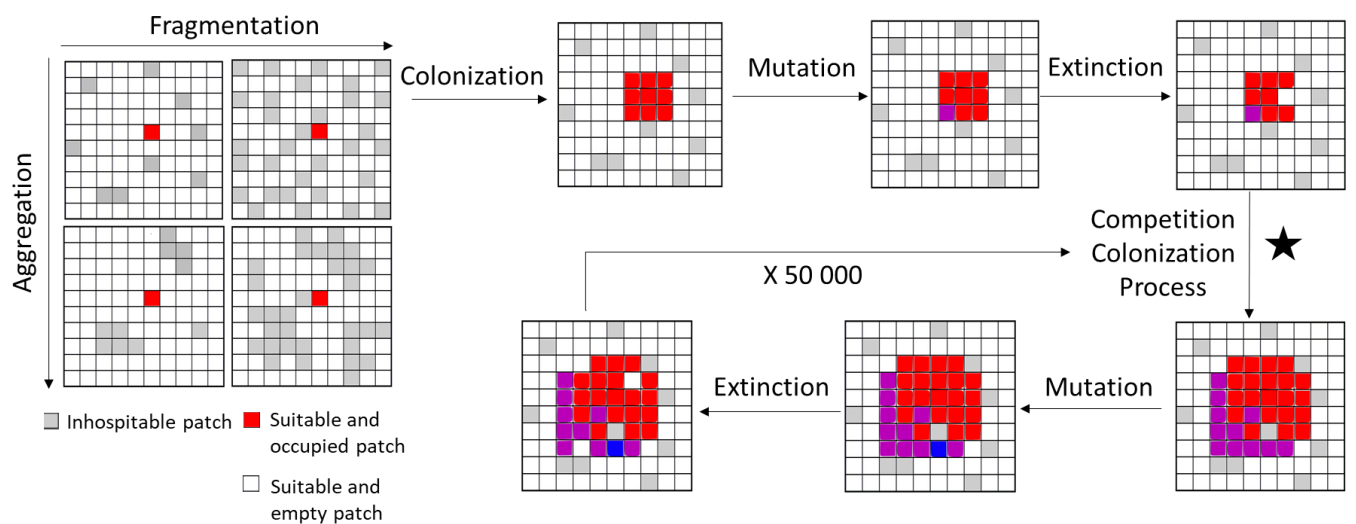
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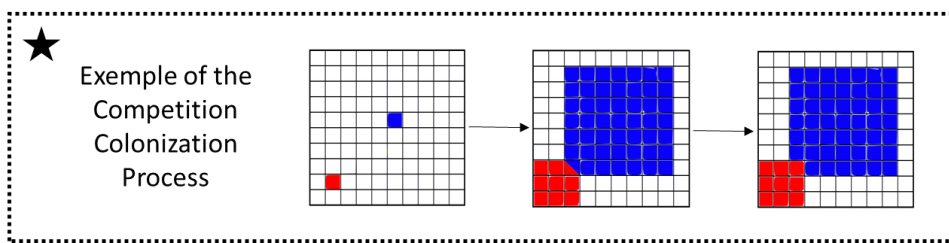
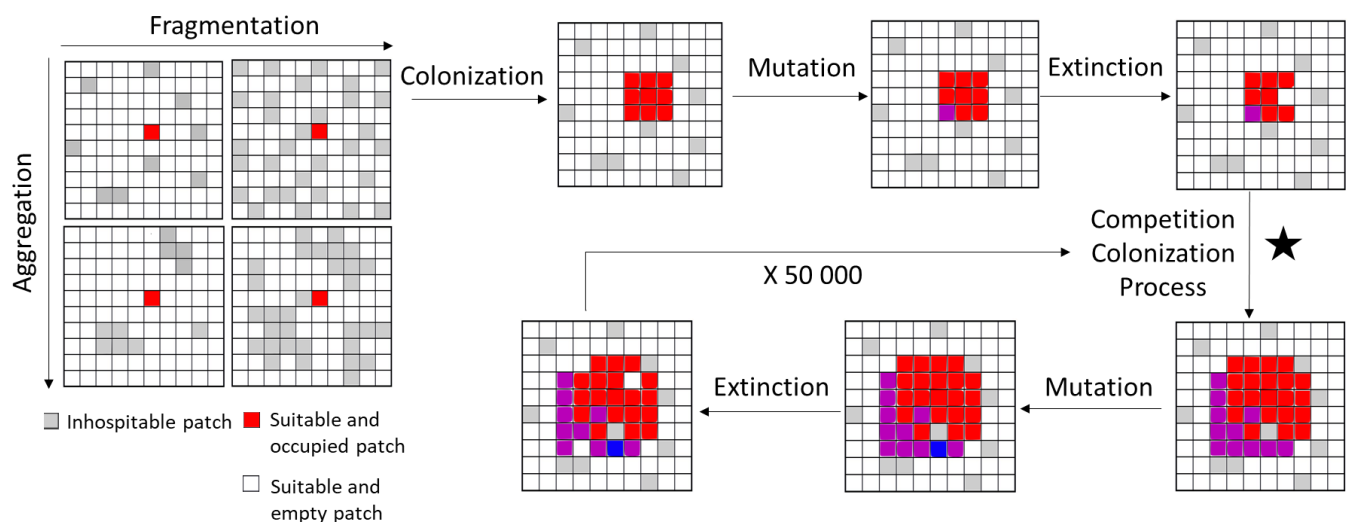
622 **Figure 3:** 2 examples of simulations showing dispersal polymorphism. (a) and (d) show the

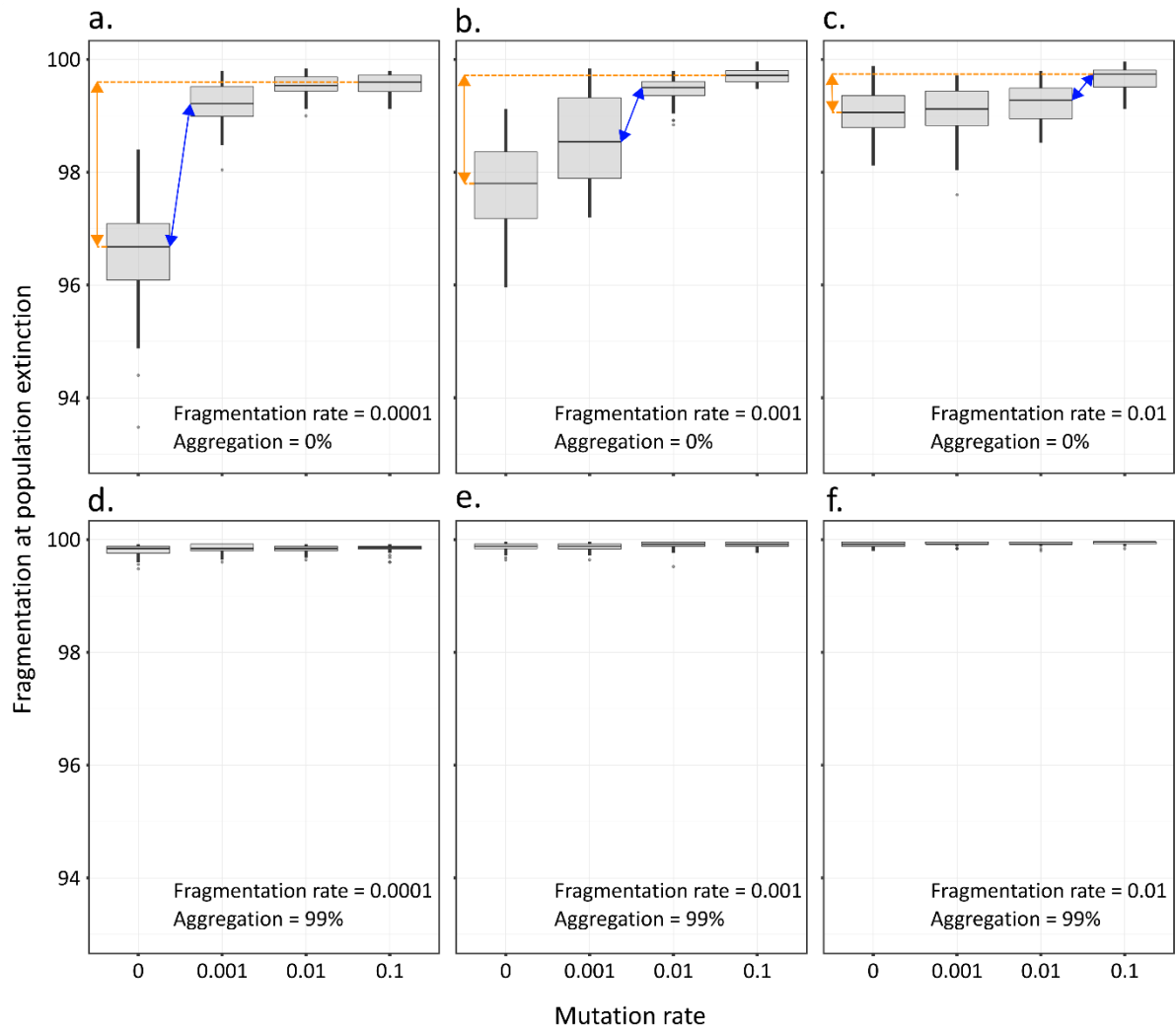
623 presence of dispersal strategies over time in two separate simulations. (b) and (e) represent the



624 grid at the end of the corresponding simulations. (c) and (f) show the relative abundance of  
 625 each strategy (mean percentage +/- SD) over the last 5 000-time steps. For (a) and (d) the  
 626 intensity of black represents the proportion of each strategy for the given time. It is log-  
 627 transformed for (d). For (b) and (e) grey patches are unsuitable, white patches are suitable and  
 628 empty, and coloured patches are suitable and occupied by populations differing in dispersal  
 629 strategies (ranging from low dispersal in red to high dispersal in blue). Dispersal strategies are  
 630 similarly color coded in panels (c) and (f). The first row of panels (a-c) shows an example  
 631 with two equally abundant dispersal distance strategies (dispersing at 5 and 9 patches).  
 632 Conditions are fragmentation of 99% and no aggregation. The second row of panels (d-f)  
 633 shows an example where one dispersal distance strategy (at 1.1 patches) dominates  
 634 (fragmentation of 95% and aggregation of 20%).

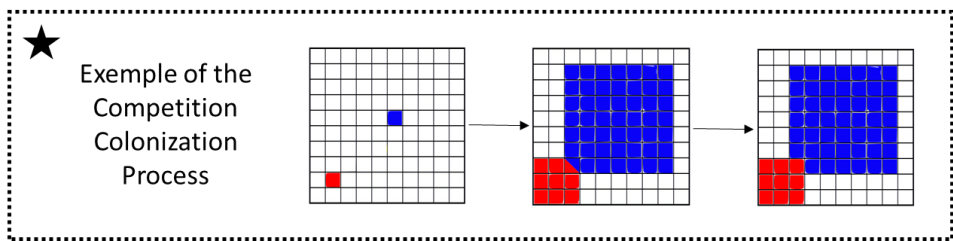
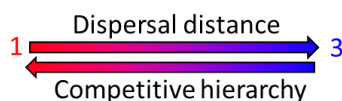
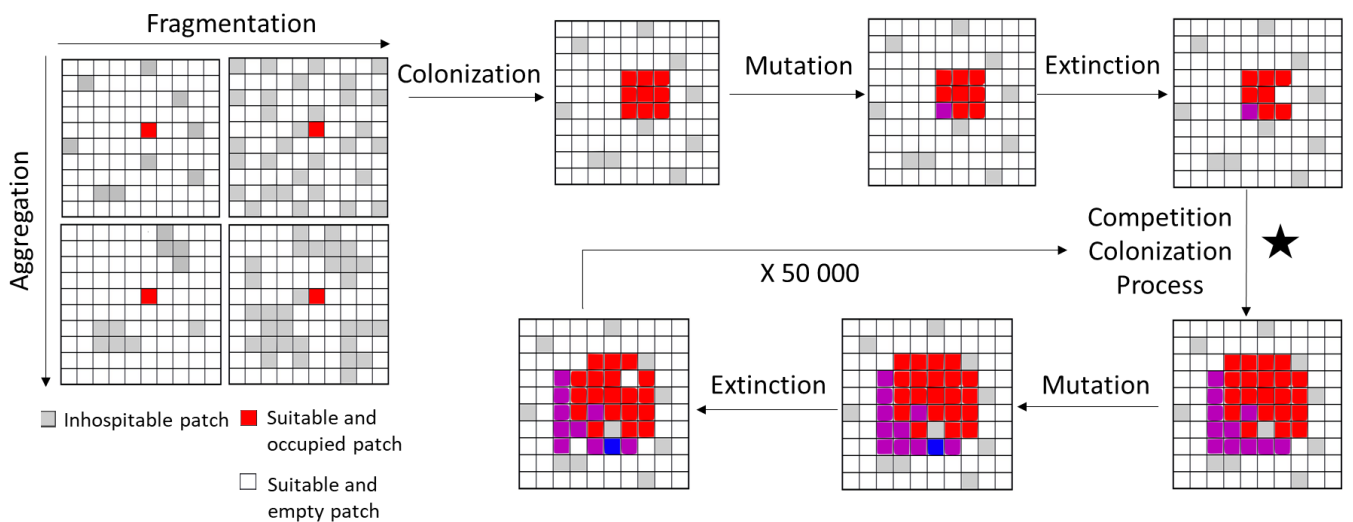
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637 **Figure 4:** Fragmentation level leading to the metapopulation extinction versus mutation rate  
 638 for different scenarios of fragmentation rate and aggregation. Orange arrows highlight the



639 difference of extinction thresholds between no evolution and fast evolution, a proxy for  
 640 maximal evolutionary rescue. Blue arrows highlight the change in mutation rate that has a  
 641 maximal effect on evolutionary rescue. Note that this occurs when mutation rates become  
 642 roughly ten times higher than fragmentation rates (a-c). Evolutionary rescue is largely  
 643 decreased in aggregated landscapes (d-f).

644

