Title: Evolution of dispersal and the maintenance of fragmented metapopulations

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ABSTRACT:

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

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

Keywords: Dispersal evolution, fragmentation, metapopulation, evolutionary rescue, spatial autocorrelation

INTRODUCTION

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

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

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

While these previous studies consider dispersal as an isolated trait, it is now widely recognized that evolutionary changes in dispersal most often imply variations in phenotypic traits that constrain other ecological interactions (Raffard *et al.*, 2022). It has been highlighted that when colonization abilities are traded against competitive abilities, coexistence of a large number of strategies is possible along this hierarchy (Tilman, 1994). Such a trade-off could for instance occur because given a fixed quantity of energy, allocation could produce a large number of small propagules (colonizer) or few large propagules (competitor) (eg, Smith and Fretwell, 1974; Geritz *et al.*, 1999). For example, the weed *Crepis sancta* produces small and/or large seeds. Small seeds have high wind dispersal due to their lightweight but low

competitiveness due to low resource storage. In contrast, large seeds have restricted dispersal due to their weight but contain more resources (Cheptou *et al.*, 2008). In social insects, dispersal and reproduction could follow from the production of many isolated queens that fly large distances and have high mortality or through the split of the colony in a few propagules that usually disperse on short distances but may be more efficient at gathering resources when founding the new colonies (Cronin *et al.*, 2013, 2016). Fragmentation affects strategies along the competition-colonization trade-off in different ways. First, it directly lowers the average density at the metapopulation level, thereby changing competitive pressures. Second, it creates isolated patches that act as a positive filter for the best dispersers. To our knowledge, only one study considers how this competition/colonization trade-off affects the dispersal strategies selected by fragmentation (Tilman *et al.*, 1994). This study shows that in a spatially variable environment with an increase of fragmentation, the more competitive (and thus the less dispersive) strategies disappear first, so that high dispersal strategies are selected.

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

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

Understanding this dispersal evolution has immediate consequences to better predict the maintenance of metapopulations. For instance, a selected increase in dispersal favors the exchange of individuals between patches and the colonization of empty patches (spatial rescue). Extinction may also be prevented when natural selection favors adapted traits, i.e. evolutionary rescue (Gomulkiewicz and Holt, 1995; Carlson *et al.*, 2014; Bell, 2017). Here, an evolutionary increase of dispersal distances could avoid a population extinction in a climate change context (Boeye *et al.*, 2012) or in a context of high mortality (Heino and Hanski, 2001). Given a temporally increasing fragmentation, natural selection may favor high dispersal, as the availability of empty and isolated patches constantly increases. Because only highly dispersive strategies can reach them, such isolated patches act as filters that favor high dispersal (Heino and Hanski, 2001). Consistent with this theoretical prediction, a temporal increase of

fragmentation led to higher dispersal in *Drosophila melanogaster* experiments (Tung *et al.*, 2018). Conversely, if evolution were to lead to less dispersal, it would potentially decrease metapopulation persistence (Gyllenberg *et al.*, 2002). The implication of the evolution of dispersal for metapopulation persistence in a world that becomes increasingly fragmented is therefore an important, unresolved issue.

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

MATERIAL AND METHODS

Our simulations consider a spatially explicit environment consisting of a grid of 50x50 patches wrapped into a torus to avoid edge effects (Fig. 1). Each patch can be in one of three

possible states: unsuitable, suitable and empty or suitable and occupied. Only suitable and empty patches are available to dispersing individuals. Importantly, we define fragmentation as the percentage of unsuitable patches. This definition of fragmentation is classically considered in the literature and is directly linked to other components often used to describe fragmentation such as the number of independent patches, their size or their isolation (Fahrig, 2003). For a given level of fragmentation, we independently vary the degree of aggregation of unsuitable patches. Examples of landscapes can be found in the upper left part of Fig. 1. Unsuitable patches are distributed randomly or with a set percentage of aggregation (created with a fractal Brownian motion) using the *NLMR* and *landscapetools* package (Sciaini *et al.*, 2018). A higher aggregation means that a suitable patch is more likely to be close to another one compared to the random expectation.

Individuals are characterized by two traits: colonization and competition capacities (both integer values) directly linked through the colonization/competition trade-off. Each time step is divided in three parts: colonization, competition and extinction (see Fig. 1).

(1) Colonization. The colonization capacity defines the radius (number of patches) of the area around the individual where its offsprings are dispersed. We assume that offspring will potentially colonize all empty but suitable patches within this range. This implicitly assumes that individuals with larger colonization capacity are not limited by the number of offspring they produce. This assumption is not biologically unrealistic. For a given amount of energy devoted to reproduction, colonizer strategies could be based on small but numerous propagules while competitive strategy would rely on a few bigger propagules (Smith and Fretwell, 1974). Plant species can for instance produce a lot of small seeds that, being light, could disperse far or few big seeds that disperse near (Cheptou *et al.*, 2008). Such a trade-off is not restricted to plants and could also apply to various animal species. Consider, for example, ant species. Some species produce

new queens that disperse alone by flying, whereas others produce new queens that disperse with a group of workers by walking. In the first case, the dispersing propagule is made of a single queen and has a long-distance dispersal while in the second case, the dispersive propagule encompasses not only the queen, but also all accompanying workers, so that its energy cost is high. In the first case, the mother colony produces a lot of new queens which is not the case in the second (Cronin *et al.*, 2013).

(2) Competition. We assume that only empty suitable patches can be colonized by propagules. Given that individuals fill all suitable surrounding patches with their offspring, suitable empty patches are often reached by several offspring simultaneously. We then assume that the competitive hierarchy favors the strategy that has the smallest dispersal distance (competition-colonization trade-off, lower part of Fig. 1). The surviving individual inherits the dispersal strategy of its parents, except in the case of rare mutation events. When mutation occurs, the dispersal range of the mutant individual is enhanced or reduced by one cell, with equal probability. We assume that established individuals (ie, occupied patches) cannot be displaced by incoming propagules, regardless of their traits.

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

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

Scenario 1: Evolution of dispersal in fixed fragmented landscapes

In the first scenario, we fix the landscape and study how dispersal evolution depends on the levels of fragmentation and aggregation. Fragmentation corresponds to a specified percentage of unsuitable patches (i.e. 0, 20, 40, 60, 80, 90, 95 or 99% of patches are assumed unsuitable). These unsuitable patches are aggregated at varying degrees (0, 20, 40, 60, or 80%). Twenty different landscapes are generated for each combination of fragmentation and aggregation. The mutation rate is set at 0.1. Each simulation lasts 50 000-time steps. Because simulations are stochastic, they never reach a completely stable equilibrium, but we checked that 50 000 time steps allowed the system to reach a stable regime that can be characterized (see examples of simulations on Fig. 2b,c,d). We record the mean dispersal capacities of individuals during the simulation and the occupancy of each dispersal strategy.

Scenario 2: Evolutionary rescue under progressively increasing fragmentation

In the second scenario, we progressively increase the level of fragmentation over time. We systematically manipulate the rates of fragmentation and of mutation to investigate conditions under which dispersal evolution can delay extinction. The grid is supposed to be fully suitable at the onset of the simulation and for the first 200-time steps. We then progressively increase fragmentation until the metapopulation becomes extinct. As in the first scenario, the increase in fragmentation occurs with random or aggregated distributions of unsuitable patches (levels of aggregation: 0%, 10%, 20%, 40%, 60%, 80%). Rates of fragmentation correspond to the probability that a suitable patch becomes unsuitable within a given time step. We tested three rates of fragmentation (0.0001, 0.001, 0.01). As evolutionary rescue is construed as a race between the speed of the disturbance and the speed of adaptation (Gomulkiewicz and Holt, 1995), we also systematically manipulate the speed of evolution by considering different rates of mutation (0.001, 0.01, 0.1). We replicate each combination of

aggregation, fragmentation rate and mutation rate forty times. We record the percentage of fragmentation at population extinction as an index of the resistance of the metapopulation to the disturbance. Higher values of this index show that evolution of dispersal allowed the metapopulation to survive higher levels of the disturbance. Evolutionary rescue occurs if metapopulations with evolution of dispersal resist higher disturbance levels than metapopulations without dispersal evolution. For each set of simulations, we also record the variations of dispersal strategies (occupancy of the various dispersal phenotypes) over time to identify the path that evolutionary rescue takes.

RESULTS

Evolution of dispersal in fixed fragmented landscapes

Higher fragmentation selects for increasing mean dispersal distances. In non-fragmented landscapes, competitive strategies eventually dominate so that dispersal distance quickly evolves close to one (Fig. *2*a and b). Such a strategy remains dominant for all low levels of fragmentation (0 to 60%). High dispersal is selected under higher fragmentation, especially strongly when fragmentation is random (7.27±1.08 patches at 99%, red line in Fig. 2a, see also Fig. 2c), which is congruent with Tilman *et al.* (1994). However, adding aggregation strongly decreases this selection effect. For instance, a little bit of aggregation (20%, orange line in Fig. 2a, see also Fig. 2d) suffices to lower the selected dispersal distance in very fragmented landscapes to 2.09±1.02 patches. Higher aggregation (40 to 80%) further decreases the selected dispersal distance, so that fragmentation hardly has any effect on selected dispersal when aggregation is high (blue lines, Fig. 2a). Aggregation therefore qualitatively changes the results of mean field models (such as Tilman *et al.*, 1994).

Evolution of polymorphism in fragmented landscapes.

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

Evolutionary rescue under progressively increasing fragmentation

When fragmentation increases over time, fast dispersal evolution allows a longer persistence of the metapopulation, i.e. an evolutionary rescue. Fig. 4 shows this evolutionary rescue as the difference (orange arrows) between the scenario with no evolution (mutation rate equal zero) and the three scenarios with more or less rapid evolution. Intuitively, evolutionary rescue occurs and is strongest when there is no aggregation, fragmentation rate is low, and mutation rate is high (mean difference of 3.04% between scenarios without and with evolution, Fig. 4a). Evolutionary rescue is largely decreased when fragmentation rate is higher (a difference of 0.63%, Fig. 4c). Variations in the potential of evolutionary rescue are not continuous. Rather, a threshold mutation rate can be identified relative to the fragmentation

rate. Under our set of parameter values, evolutionary rescue occurs when the mutation rate is ten times higher than the fragmentation rate (Fig. 4a,b,c, blue arrows). Finally, we stress that aggregation largely constrains evolutionary rescue. No potential for evolutionary rescue can be identified in aggregated landscapes (Fig. 4d,e,f).

DISCUSSION

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

The selection of more dispersive strategies in fragmented landscapes in a context of competition/colonization trade-offs is congruent with Tilman *et al.* (1994) which also relies on this trade-off. Other studies on the evolution of dispersal in spatially heterogeneous systems, but in the absence of a competition/colonization trade-off, show a reverse pattern, as dispersal is then counter selected because dispersal costs are enhanced by spatial heterogeneities (Hastings, 1983; Travis and Dytham, 1999). This highlights that patterns of selection strongly depend on the trade-off structure associated with dispersal traits. Recent works highlight the importance of dispersal syndromes (Stevens *et al.*, 2014; Raffard *et al.*, 2022), i.e. the fact that dispersal traits may be directly coupled to traits defining ecological interactions. The

competition/colonization trade-off falls within this category, as variations of dispersal are directly coupled to competition hierarchies. Our results therefore highlight how such a syndrome could lead, for some landscapes, to the selection of higher dispersal, while works that consider evolution of dispersal alone (eg, Hastings, 1983; Travis and Dytham, 1999) would produce the reverse pattern. Application of either framework of course depends on the types of organisms that are considered and whether dispersal traits are competitively costly.

We explain the selection of higher dispersal in fragmented landscapes by two mechanisms. First, fragmentation decreases overall occupancy, thus reducing the average competition level. The advantage of competitive strategies is therefore reduced. Second, fragmentation intensifies the strength of the competition for space which favors colonizers. Isolated patches in fragmented landscapes can only be exploited by highly dispersive strategies. Effects of fragmentation on mean levels of dispersal have led to contrasted results in empirical studies (Cheptou *et al.*, 2017). Our results of a selection of higher dispersal is for instance coherent with empirical studies of nuthatches (*Sitta europaea*) in Belgium (Matthysen *et al.*, 1995). Similarly, metapopulation study of the Glanville fritillary in Finland shows that isolated patches of the metapopulation act as positive filters for the more dispersive strategies (Hanski *et al.*, 2004) and that this variation can be linked to allelic variations constraining flight metabolism (Haag *et al.*, 2005). Conversely, a decrease of dispersal at higher fragmentation levels has been observed in various animal or plant species (Schtickzelle *et al.*, 2006; Bonte *et al.*, 2006; Cheptou *et al.*, 2008). Spatial heterogeneity and competition decrease are two forces that act with opposite effects, the former decreasing dispersal (higher dispersal cost) while the latter increases it (decreased abundancies in fragmented landscapes, relax competition). The importance of each force varies among species and needs to be systematically considered to better predict changes in dispersal.

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

We observe dispersal polymorphism when fragmentation is high and aggregation low to intermediate. Such landscapes contain a mix of large aggregates of patches and of isolated patches. The strategy favored in the aggregates of patches is more competitive, and the dispersal distance selected there depends on how loose the aggregates are. When aggregation produces continuous aggregates, the most competitive strategies are favored (dispersal distance close to 1, Fig. 3f), while when aggregates are looser, selected dispersal distances could be higher (Fig. 3f). In all cases, isolated patches favor more dispersive strategies. These results are coherent with previous theoretical studies that show how fragmentation can favor dispersal

polymorphism. In particular, some of them showed that polymorphism is prevalent when few large patches (our patch aggregates) co-occur with small patches (our isolated patches) (Parvinen, 2002; Bonte *et al.*, 2010; Massol *et al.*, 2011; Parvinen *et al.*, 2020).

Evolutionary rescue can be construed as a race between speed of adaptation and of environmental deterioration. Hence, the faster the evolution and the slower the perturbation, the more likely the rescue. We observe that such expectations are met when fragmentation is random (no aggregation). Dispersal evolution delays the extinction of the population when fragmentation rate is low and mutation rate high. Fast selection of good dispersers then occurs. As these are adapted to occupy isolated patches, such strategies foster spatial rescue in the highly fragmented landscapes. Slow evolution would not allow that. At the onset of fragmentation, the grid is continuous, and mostly occupied by competitors. If fragmentation is too fast, there is no time for dispersers to appear and become selected and to fill isolated patches. Interestingly, our study shows that rescue happens as a threshold phenomenon, being only possible when mutation rates are higher (10 times higher in our model) than perturbation rates. No evolutionary rescue occurs when fragmentation is aggregated, for two reasons. First, aggregation delays extinction by itself even without evolution. Under high fragmentation and aggregation levels, suitable patches make small continuous groups that facilitate the local persistence of competitors. Second, in an aggregated context, dispersal evolution is absent or strongly constrained (blue curves on Fig. 2a) so that little evolutionary potential exists. In the absence of such an adaptive potential, evolutionary rescue cannot act. Our results on the possibility of rescue through evolutionary changes of dispersal agree with former theoretical works where fragmentation either stemmed from climatic changes (Boeye *et al.*, 2012) or from heterogeneities in mortality (Heino and Hanski, 2001). While in the actual context of fast environmental changes, it may seem complicated for species to evolve quickly enough (10 times faster than the perturbation), several examples of fast evolution of dispersal in fragmented

systems have been reported (reviewed in Cheptou *et al.*, 2017). Whether such evolutions are sufficient to affect long term metapopulation persistence is however unknown. The fact that evolutionary rescue does not happen here in aggregated landscapes also has important implications. The current fragmentation of habitats is a complex non-random process that may be frequently auto-correlated in space, therefore producing aggregated structures. For instance, the construction of additional urban areas next to existing urban areas creates aggregated landscapes. Studies from the Tabriz Metropolitan Area (Iran) show that the destruction of suitable habitats surrounding the cities result in the creation of aggregated non-suitable patches (Dadashpoor *et al.*, 2019a, 2019b). Aggregation of fragmentation can also be linked to the displacement and development of agricultural activities. In Beijing City, China, landscape patterns show important and complicated changes in the distribution of urban and agricultural lands. Economic development expands cultivated land and construction into forests and grasslands resulting in aggregated and less diverse landscapes (Li *et al.*, 2017). We propose that when fragmentation happens in such aggregated ways, evolution will likely play a minor role in the maintenance of the metapopulation.

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

evolution and its implications for the future of biodiversity.

FIGURES

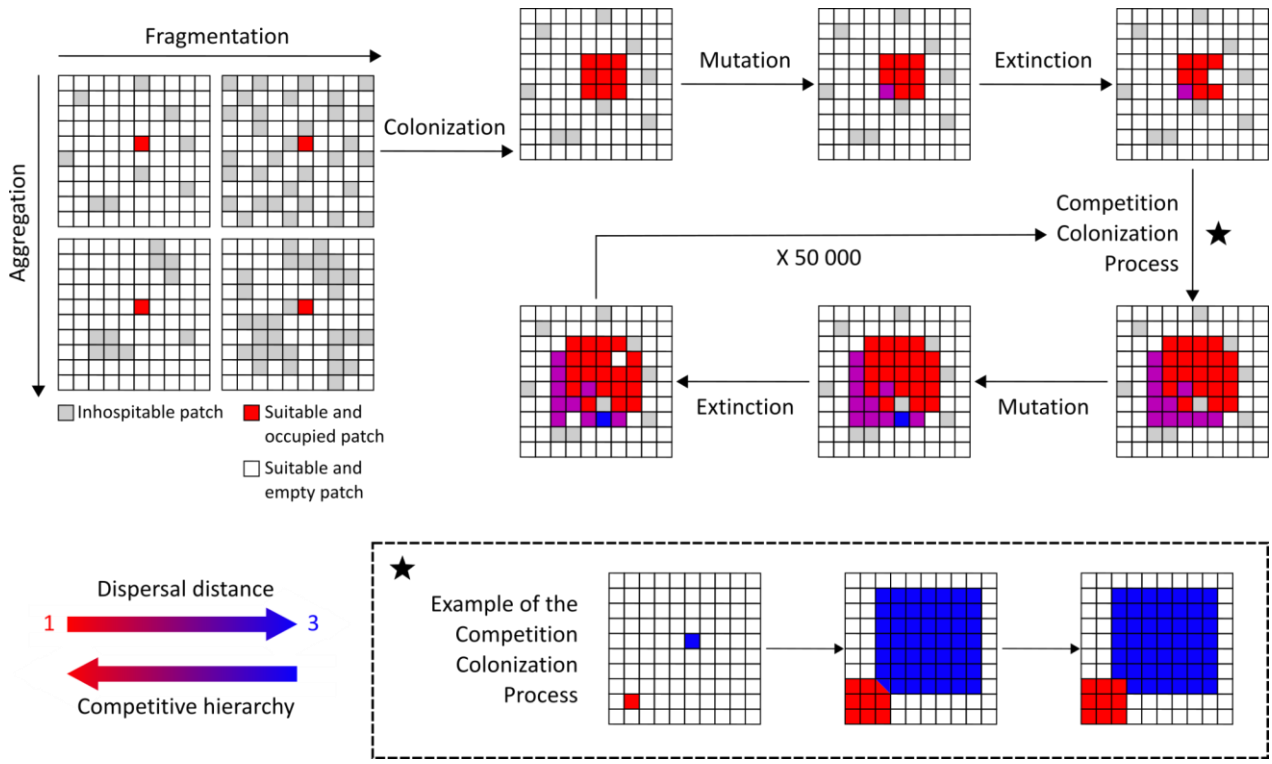

Figure 1: Illustration of a simulation in the context of the competition/colonization tradeoff in a fixed environment scenario. The box represents the competition/colonization process when two individuals arrive on the same patch.

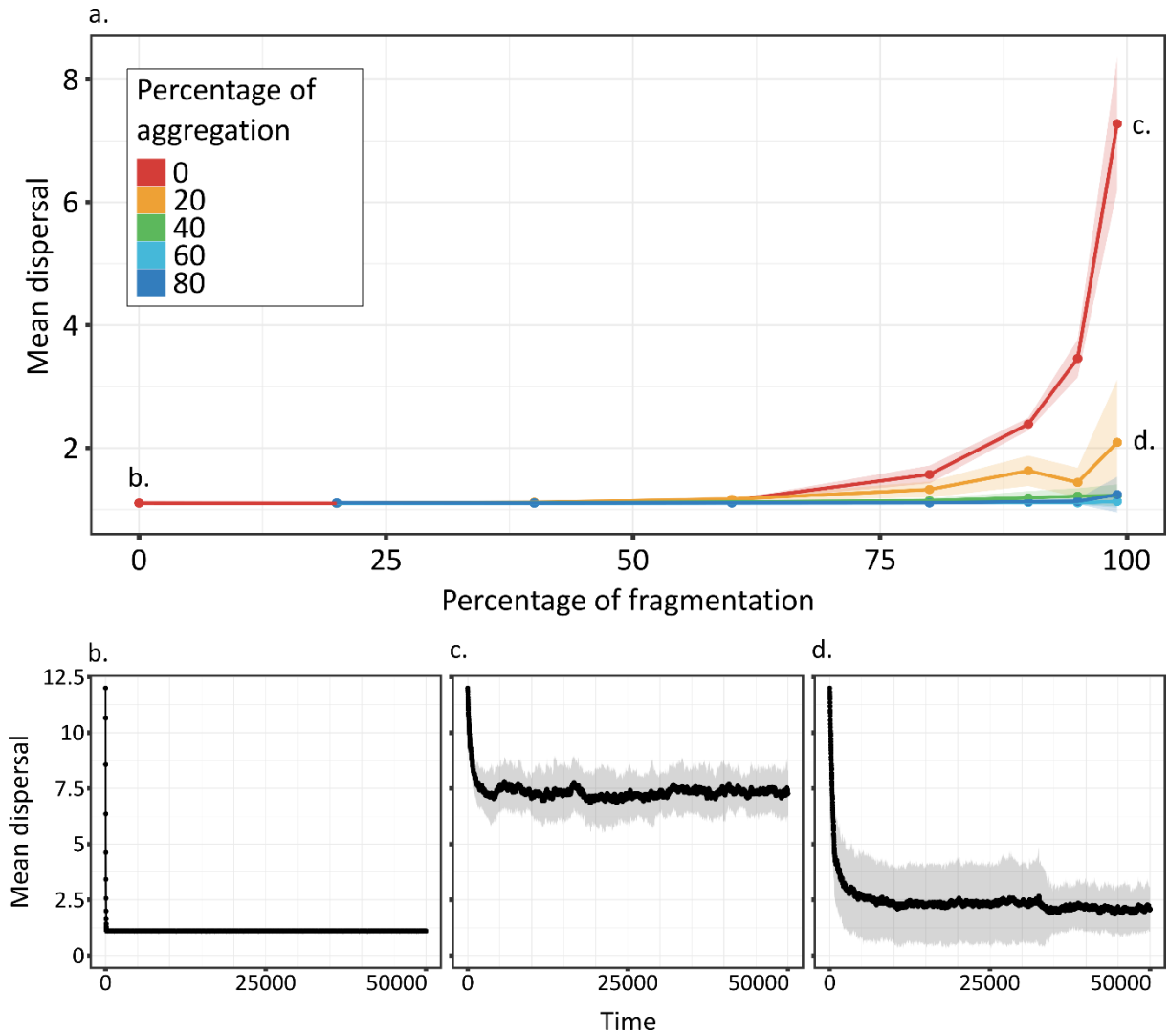

Figure 2: Dispersal (mean +/- SD) at the end of simulations (at equilibrium) versus environment fragmentation and aggregation (a), and over time for the 20 replicates for conditions of no fragmentation and no aggregation (b), 99% of fragmentation and 20% of aggregation (c) or 99% of fragmentation and no aggregation (d).

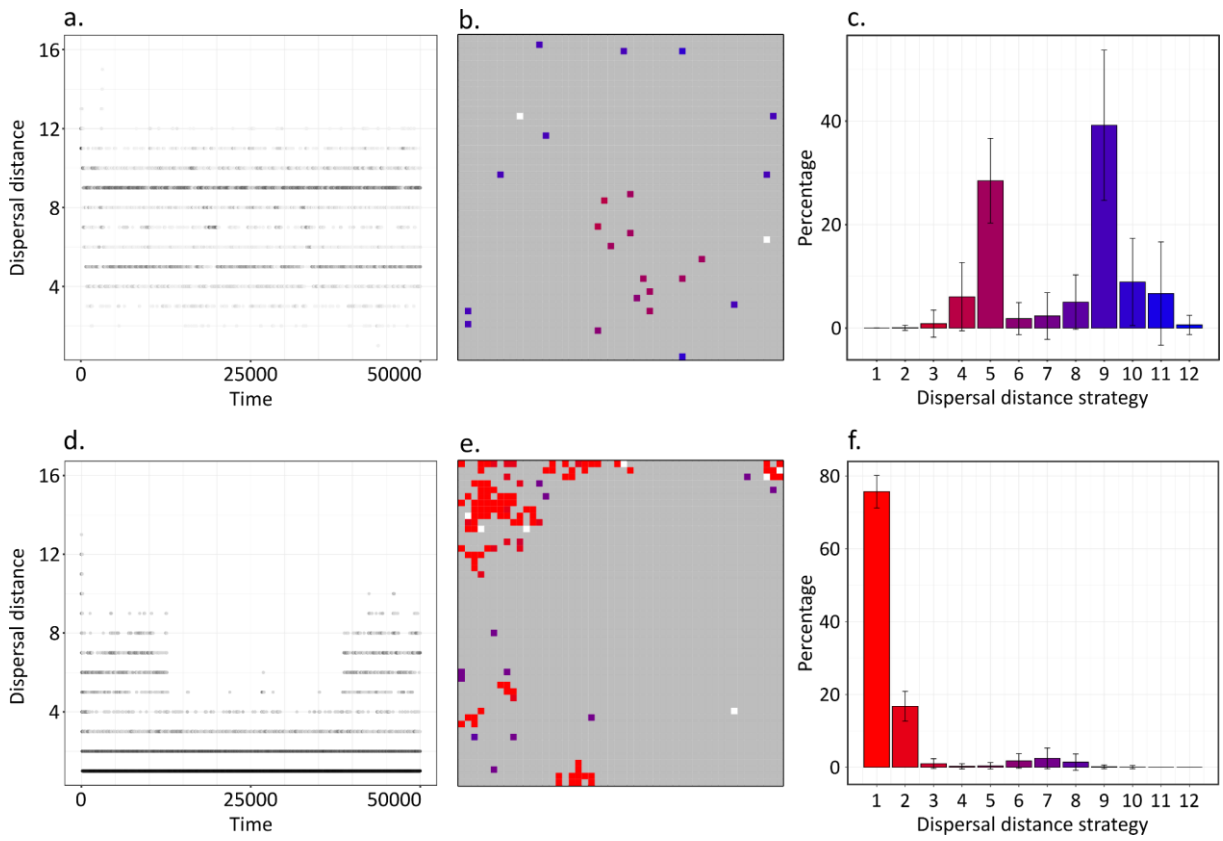

Figure 3: 2 examples of simulations showing dispersal polymorphism. (a) and (d) show the presence of dispersal strategies over time in two separate simulations. (b) and (e) represent the grid at the end of the corresponding simulations. (c) and (f) show the relative abundance of each strategy (mean percentage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

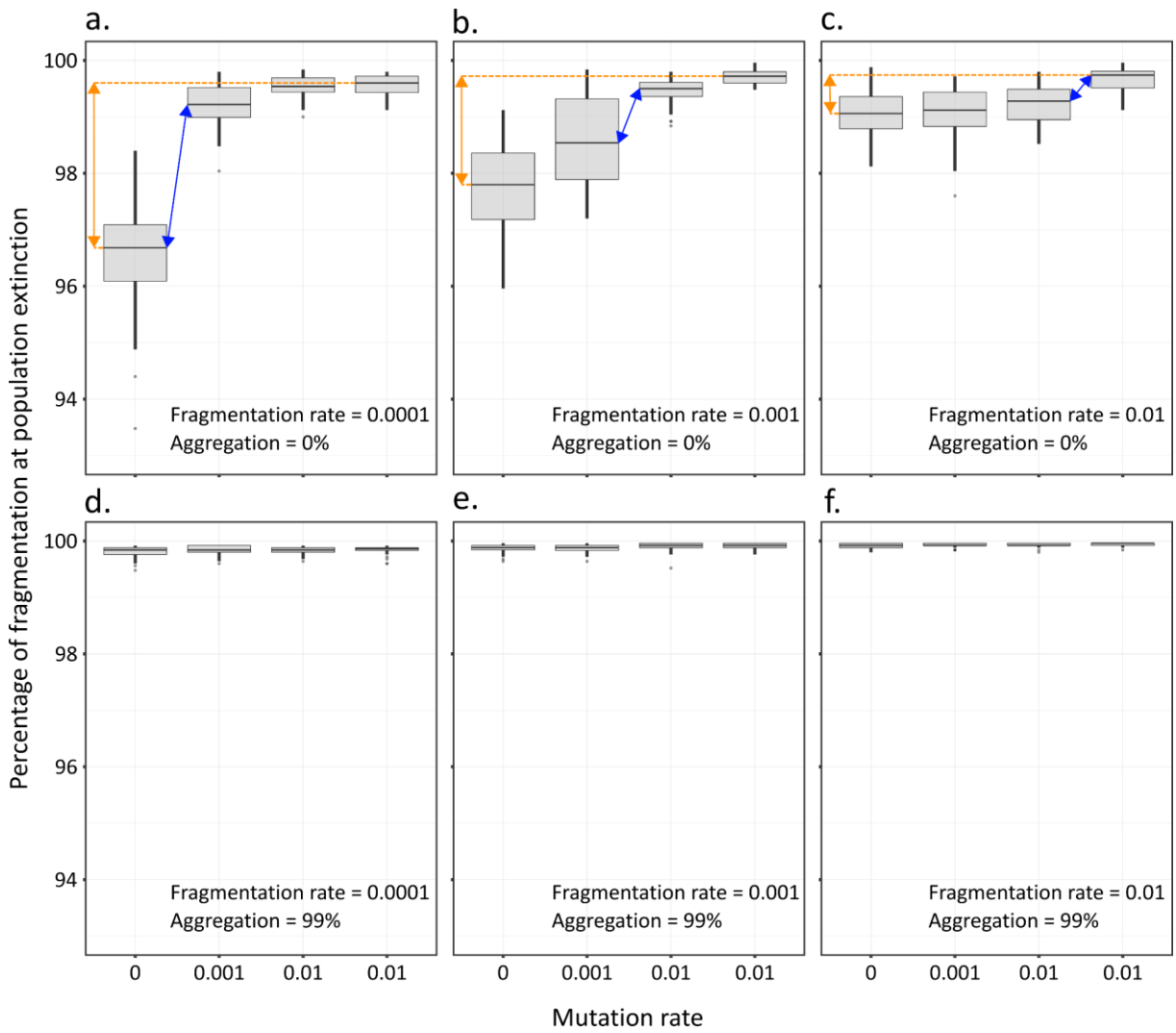

Figure 4: Percentage of fragmentation at population extinction versus mutation rate, fragmentation rate and aggregation. Orange arrows represent the difference of fragmentation at population extinction between no evolution and fast evolution. Blue arrows represent the steps between the two mutation rates where there is a difference in fragmentations at population extinction, i.e., where the mutation rate is ten times higher than the fragmentation rate.

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