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1 **Title**

2 Clustered or scattered? The impact of habitat fragmentation on establishment and early spread

3

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11

12

13 **Abstract**

14 Habitat quality is a major predictor of establishment success for an introduced species.
15 Yet, introduction areas are usually landscapes, i.e. heterogeneous sets of habitats that are more
16 or less favourable to the introduced species. As individuals are likely to disperse as soon as they
17 are introduced, the quality of the habitat surrounding the introduction site is as critical to the
18 persistence of introduced populations as the quality of the introduction site itself. Moreover,
19 demographic mechanisms such as Allee effects or dispersal mortality can also hamper dispersal
20 and affect spread across the landscape, in interaction with the spatial distribution of favourable
21 habitat patches. In this study, we investigate the impact of fragmentation, defined as the degree
22 of scattering of a constant amount of favourable habitat, on establishment and early spread.
23 First, we simulated introductions in one-dimensional landscapes for different dispersal rates
24 and either dispersal mortality or Allee effects. The landscapes differed by the fragmentation of
25 favourable habitats, which were either “clustered” into few large aggregates or “scattered” into
26 multiple smaller ones. Second, we tested the predictions of simulations by performing
27 experimental introductions of hymenopteran parasitoids (*Trichogramma chilonis*) in
28 "clustered" and "scattered" microcosm landscapes. Results highlighted two impacts of
29 fragmentation. By increasing the risks of dispersal from the introduction site to unfavourable
30 habitat early during the invasion, fragmentation decreased establishment success. However, by
31 decreasing the distance between favourable habitat patches, it also improved the subsequent
32 spread of introduced species over larger areas.

33

34 **Introduction**

35 Establishment is a crucial phase of biological invasions, which determines whether the
36 introduced populations turn into self-sustaining colonies likely to spread or go extinct
37 (Blackburn et al. 2011). The match between the characteristics of the introduced species and

38 the environmental conditions they experience in their new habitat is a major predictor of
39 establishment success (Shea and Chesson 2002, Moles et al. 2008). Yet, introduction areas are
40 usually natural landscapes, made up of habitats of different quality (Turner et al. 2001).
41 Establishment can be affected by the heterogeneity of the introduction area (Melbourne et al.
42 2007), as well as the spatial distribution of these habitats of different quality (Schreiber and
43 Lloyd-Smith 2009). This study focuses on the impact of habitat distribution in terms of
44 fragmentation. The denomination of “fragmentation” is widely used, to convey different
45 meanings depending on the context. Following Fahrig (Fahrig 2003), we consider it here as the
46 scattering of favourable habitat without habitat loss. Therefore, it describes a particular structure
47 of habitat distribution at the landscape scale: a given amount of favourable habitat will be
48 broken apart in fragmented landscape but aggregated into large clusters in a non-fragmented
49 one (McGarigal and Cushman 2002, With 2002).

50 The impact of fragmentation on invasion success is linked to colonisation, which is not
51 only essential for spread, but also for establishment. Introduced populations are known to have
52 high extinction risks because of their small initial size (Simberloff 2009), and emigrations from
53 the introduction site will slow down their growth, thus increasing this risk further (Kean and
54 Barlow 2000, Parlato and Armstrong 2013). Dispersal can nevertheless be beneficial as it
55 allows the creation of new colonies, and increase overall persistence in the long run (Morel-
56 Journel et al. 2016). These effects of dispersal on establishment are tightly linked to the spatial
57 structure of the introduction area, and in particular its level of fragmentation. Simulation results
58 by Schreiber and Lloyd-Smith (2009) indicate that individuals introduced in favourable habitat
59 have higher chances of dispersing to less favourable habitat if the landscape is fragmented.
60 Dispersing individuals are then less likely to colonize new habitat patches. In less fragmented
61 landscapes, a favourable introduction site is more likely to be in a larger cluster of favourable
62 habitat patches (Schreiber and Lloyd-Smith 2009), and thus safer for emigrating individuals.

63 However, fragmentation can also facilitate early colonisation across larger spatial scales, as the
64 breaking apart of habitat tends to reduce the mean distance between the patches of favourable
65 habitat (Fahrig 2003, Roques and Chekroun 2010). It therefore increases the probability of
66 successfully dispersing to those habitats, and form new colonies. In a theoretical study,
67 Dewhurst and Lutscher (2009) thus indicate that aggregating resource into larger and more
68 isolated clusters can prevent spread. It is therefore possible to identify two spatial scales at
69 which fragmentation has two different impacts: decreasing persistence of populations in the
70 direct surroundings of the introduction site, and increasing colonisation in the rest of the
71 landscape.

72 These opposite effects of fragmentation on dispersal will likely be affected by
73 demographic processes that shape colonization dynamics in heterogeneous environments.
74 Mechanisms such as dispersal mortality or Allee effects create additional costs to dispersal that
75 make colonisation more difficult. Dispersal mortality eliminates dispersing individuals, thus
76 reducing the chances that some of them reach favourable habitat to colonise. On the other hand,
77 Allee effects can bring small populations to extinction at low densities (Allee 1949, Courchamp
78 et al. 2008), and prevent colonisation if the number of individuals dispersing to a new patch is
79 too low (Keitt et al. 2001). By affecting colonisation success these mechanisms are susceptible
80 to exacerbate the effects of fragmentation.

81 Although fragmentation has been identified theoretically as a key element of landscape
82 structure as regards to the dynamics of expanding invasive populations, experimental
83 confirmations of the impact of resource distribution on the establishment and spread of
84 introduced populations remain scarce. This study aims at bridging this gap between theory and
85 empirical data by investigating the role of fragmentation with both simulations and
86 experimental results. First, we developed a simple model describing a biological invasion in a
87 spatially explicit context. We designed heterogeneous one-dimensional landscapes with

88 alternating “bad” and “good” patches, according to their quality, and centred around the
89 introduction site. Two fragmentation levels were considered: “scattered” landscapes (high
90 fragmentation level) alternated one good one bad patch, and “clustered” landscapes (low
91 fragmentation level) alternated three good and three bad patches (Figure 1A, B). We simulated
92 invasions in these landscapes for different dispersal rates, combined with either dispersal
93 mortality or Allee effects. Then, we tested the predictions from the model by monitoring
94 artificial introductions of the hymenopteran parasitoid *Trichogramma chilonis* in artificial
95 landscapes with the same structure, with two levels of fragmentation and dispersal mortality.

96

97 **Methods**

98 *Structure of the landscape*

99 The heterogeneity studied in the introduction area was created with two kinds of patches
100 with different resource levels: “bad” patches with a low carrying capacity (K_1) and good patches
101 with high carrying capacity (K_2). The difference between the two patches qualities was set to
102 $K_2 = 5K_1$, to ensure significant differences between the two treatments. Those patches were
103 arranged as a linear chain according to a one-dimensional stepping stone model (Figure 1A, B).
104 Fragmentation was created by alternating good and bad patches along the spatial axis: scattered
105 landscapes alternated one good one bad patch, while clustered landscapes alternated three good
106 and three bad patches. Although the pattern could theoretically repeat infinitely, we focused
107 here on establishment and early dispersal, occurring in the surroundings of the introduction site
108 only. Therefore, our landscapes were made up of eleven patches (five good and six bad), with
109 the introduction site (a good patch) in the centre. Those landscapes structures were used for the
110 simulations as well as the experiments.

111

112 *Model and simulations*

113 The model used here is adapted from Morel-Journel et al. (2016) and describes the
 114 dynamics of a population in a one-dimensional stepping-stone landscape W . This model aims
 115 at describing general population dynamics and bringing insight on invasion dynamics
 116 regardless of the species considered.

$$117 \quad N_{i,t+1} = f\left(\sum_{j \in W} M(i,j)N_{j,t}\right), \quad (1)$$

118 with $N_{i,t}$ the population size at generation t and location i in the landscape W . The value of $N_{i,t}$
 119 is systematically truncated to the nearest integer and the population is considered extinct for
 120 $N_{i,t} < 1$. This model comprises two successive phases: (i) a dispersal phase associated with the
 121 dispersal kernel $M(i,j)$ describing the probability that an individual disperses from locations j
 122 to i and (ii) a growth phase, with $f(\cdot)$ a function describing the growth of the population at
 123 location i after dispersal.

124 At each dispersal phase, the probability that an individual disperses from patch j to patch
 125 i thus depends on their distance:

$$126 \quad M(i,j) = \begin{cases} 1 - 2d_{j,t}, & |i - j| = 0 \\ (1 - m)d_{j,t} & |i - j| = 1, \\ 0, & |i - j| = 2 \end{cases} \quad (2)$$

127 where $d_{j,t}$ is the probability that an individual disperses to one of the neighbouring patches and
 128 m accounts for dispersal mortality. Individuals can only stay in their own patch ($|j - i| = 0$),
 129 or disperse to an adjacent patch ($|j - i| = 1$). This limited kernel allows us to focus on short-
 130 distance dispersal, and corresponds to the dispersal behaviour also observed in the experimental
 131 setup used conjointly with the simulations. The growth phase is described by a Ricker model
 132 including an Allee effect (Courchamp et al. 1999, Brassil 2001):

$$133 \quad f(x) = x e^{r\left(1 - \frac{x}{K}\right)\left(1 - \frac{A}{x}\right)}, \quad (3)$$

134 when $x \geq 1$ and $f(0) = 0$. Here r is the per capita growth rate and A is the Allee threshold. There
 135 is no Allee effect when $A = 0$, a weak Allee effect when $0 < A < 1$ and a strong Allee effect
 136 when $A > 1$. We added a normally distributed noise ε to the deterministic growth rate in (3) to

137 take demographic and environmental stochasticities into account (Lande et al. 2003):

$$138 \quad f(x) = x e^{r \left(1 - \frac{x}{K}\right) \left(1 - \frac{A}{x}\right) + \varepsilon}, \quad \varepsilon \sim N \left(0, (\sigma^2, \sigma_e^2 + \frac{\sigma_d^2}{x})\right). \quad (4)$$

139 σ_e^2 and $\frac{\sigma_d^2}{x}$ correspond to variability in the population growth rate respectively caused by
140 environmental and demographic stochasticity. As demographic stochasticity stemmed from the
141 variability in individual fitness, its effect on the population growth rate was averaged over the
142 whole population: if the variance in individual fitness from one individual to the other was the
143 resulting variance at the population scale was $\frac{\sigma_d^2}{x}$.

144 The model was used to simulate introductions the landscape described in the previous
145 section, for $K_1 = 60$, so that populations around carrying capacity would be safe from potential
146 Allee effects, and $K_2 = 300$ to maintain the 1:5 ratio between K_1 and K_2 . We followed the
147 invasions during 10 generations, for different values of dispersal rate ($d_{j,t}$ varying between 0
148 and 0.4) and a mechanism adding a cost to colonisation : either an Allee effect (A varying
149 between 0 and 10) or dispersal mortality (m varying between 0 and 1). Because the model is
150 stochastic, each combination of parameters was simulated 1000 times for $r = 1$, $\sigma_e^2 = 0.1$ and
151 $\sigma_d^2 = 0.1$. For each simulation, the maximal extent of the metapopulation was computed as the
152 number of good patches colonized outside of the introduction site.

153

154 *Experiment*

155 In complement of the simulations, we performed introductions of the parasitoid wasps
156 *Trichogramma chilonis* (*Hymenoptera: Trichogrammatidae*) in artificial landscapes with the
157 structures described previously, and monitored the dynamics over ten generations. Each
158 generation lasted nine days, including two days of adult life, after which the adults were
159 manually removed from the experiment to maintain non-overlapping generations. During their
160 adult life, individuals were able to move freely between patches by going through corridors.

161 According to previous experiments in similar conditions (Morel-Journel et al. 2016), they were
162 expected to disperse at most from one patch to an adjacent one during their adult life. Resource
163 was provided in the form of eggs of the Mediterranean flour moth *Ephestia kuehniella*
164 (*Lepidoptera: Pyralidae*) for *T. chilonis* to parasitize. As only one individual is usually able to
165 fully develop from one host (Suzuki et al. 1984), the carrying capacities in the experiment were
166 controlled by the number of hosts available. Good patches were provided with approx. 450 eggs
167 at each generation, as previous experiments by Vercken et al. (2013) indicate that *T. chilonis*
168 populations would reach carrying capacities around 300 individuals in these conditions. The
169 bad patches were provided with approx. 90 eggs to maintain the 1:5 ratio between K_1 and K_2 .
170 The larvae developing within *E. kuehniella* eggs would eventually turn dark because of the
171 chitinisation of the parasitoid pupae (Reay-Jones et al. 2006). Parasitized eggs were then
172 counted on photograph with the ImageJ software (Rasband 1997) and their number was
173 considered a reliable proxy of the number of adults in the next generation. Data obtained
174 through the monitoring of parasitized eggs counts were subsequently analysed with the R
175 software (R Core Team 2015).

176 We set up a 2 x 3 factorial design for the experiment, with the two fragmentation levels
177 (scattered and clustered) and three levels of dispersal mortality. All the combinations were
178 replicated in twelve experimental blocks, for a total of 72 experimental introductions. We only
179 considered one type of cost to dispersal to increase the number of experimental replicates and
180 have more statistical power in the analyses. Dispersal mortality was chosen over a demographic
181 Allee effects, which is more species-dependent and less widespread in empirical data (Kramer
182 et al. 2009, Gregory et al. 2010), despite a large use in theoretical studies. We were able to
183 manipulate dispersal mortality by adding optional dead-end exits to the pipes connecting
184 adjacent patches. Those dead-ends made successful dispersal to neighbouring patch less likely,
185 as individuals stayed in these dead ends without finding the next patch (results not shown). Two

186 adjacent patches were thus connected with either (i) two regular pipes for low dispersal
187 mortality, (ii) one regular and one pipe with a dead-end exit for medium dispersal mortality,
188 (iii) two pipes with dead-end exits for high dispersal mortality (Figure 1C, D, E).

189 To accurately characterise the impact of heterogeneity itself in the landscape, we
190 computed the extinction rates of good and bad patches (as the number of extinctions over the
191 number of colonisations for each replicate), and compared them using a paired Wilcoxon test.
192 As we expected to observe different effects of fragmentation on early invasion at two different
193 spatial scales, we characterized (i) the surroundings of the introduction site as the two good
194 patches closest to the introduction site and (ii) in the rest of the landscape as the two good
195 patches furthest from the introduction site. We computed the surroundings and landscape
196 occupancy rates as the proportion of replicates in which at least one good patch was colonised,
197 in the surroundings and the rest of the landscape respectively. The surroundings occupancy rate
198 was analysed with a binomial general linear mixed model, the experimental block as a random
199 effect. Model averaging was over the candidate models according to their AIC_C (Grueber et al.
200 2011): (i) without any fixed factor, (ii) with dispersal mortality as a factor, (iii) with landscape
201 fragmentation as a factor, (iv) with the additive effect of both factors (Supplementary Material).
202 As there were very few colonisations in the rest of the landscape, the landscape occupancy rate
203 was analysed with Fisher's exact tests.

204

205 **Results**

206 In accordance with our predictions, we observed an overall positive relationship
207 between colonisation and the dispersal rate, and a negative relationship between colonisation
208 and the mechanism creating additional costs to colonisation, i.e. Allee effects or dispersal
209 mortality (Figure 2). The impacts of the two mechanisms on colonisation were similar. By
210 comparing colonisation rates in scattered and clustered landscapes, we evidenced parameter

211 combinations for which colonisation was affected by the fragmentation level. For high
212 colonisation costs and very low dispersal rates, populations in clustered landscapes performed
213 better than those in scattered landscapes: the first managed to colonise the surroundings of the
214 introduction site, i.e. the three patches of local cluster while the second only colonised the
215 introduction site. In contrast, for intermediate dispersal rates and low colonisation costs,
216 populations in clustered landscapes achieved lower colonization than those in scattered
217 landscapes: the first only colonised the surroundings of the introduction site while the others
218 managed to colonise the rest of the landscape.

219 Experimental results confirmed the impact of habitat quality on local population
220 dynamics, as the bad patches had a significantly higher extinction rate than the good ones
221 (paired Wilcoxon test, $V = 706.5$, $p < 0.001$). We also observed clear patterns concerning the
222 colonisation (Figure 3). We assessed the occupancy rate of the good patches surrounding the
223 introduction site, and in the rest of the landscape separately. The fragmentation level affected
224 negatively the surroundings occupancy rate (Wald test, $z = 4.282$, $p < 0.001$), but positively the
225 landscape occupancy rate (Fisher's exact test, $p = 0.025$). Thus, populations introduced in
226 clustered landscapes managed to colonise the patches surrounding the introduction site more
227 often than those in scattered landscapes, but did not manage to successfully colonise the good
228 patches outside of their local cluster. Finally, we evidenced a negative impact of dispersal
229 mortality on the surroundings occupancy rate (Wald test, $z = -2.243$, $p = 0.025$), but not on the
230 landscape occupancy rate (Fisher's exact test, $p = 0.865$).

231

232 **Discussion**

233 Simulation and experiment results confirm the twofold impact of the fragmentation
234 level of the landscape on invasion success, depending on the costs associated with dispersal.
235 Breaking apart a constant amount of favourable habitat in small fragments in the landscape

236 reduced the formation of colonies close to the introduction site, while facilitating dispersal over
237 larger scales. When colonisation was not impaired (when the costs of dispersal were low or
238 inexistent), simulation results indicated that fragmentation could facilitate colonisation at larger
239 scales by reducing the maximal distance between good habitat patches. These results were
240 consistent with the patterns observed during the experiment. Indeed, the only recorded
241 colonisations of the furthest patches from the introduction site occurred in scattered landscapes.
242 They also concur with earlier theoretical work on the positive effect of fragmentation on
243 invasive spread (With 2002, Fahrig 2003). Indeed, fragmentation can provide stepping stones,
244 which increase connectivity within a landscape (Schippers et al. 2008, Saura et al. 2014). When
245 the costs associated with dispersal were higher, the impact of fragmentation became deleterious
246 to colonisation. Dispersal mortality and Allee effects increased the minimal number of
247 dispersing individuals necessary to successfully colonise patches, respectively by eliminating
248 some of them during dispersal and by raising the minimal initial population size necessary to
249 ensure colonisation. The presence of bad patches, harbouring fewer individuals, around the
250 introduction site in scattered landscapes, did not prevent colonisation of other good patches
251 altogether, although it made it more difficult. This conclusion is supported by the lower
252 colonisation rate of the surroundings of the introduction site observed during the experiments
253 in the scattered landscapes.

254 In previous studies on the subject, bad patches were characterized by a negative
255 population growth rate (Lutscher et al. 2006, e.g. Dewhurst and Lutscher 2009) and so acted
256 like barriers to dispersal. In our study, heterogeneity was created by the carrying capacity.
257 Therefore, they could harbour populations, although smaller than those in good patches, and
258 much more prone to stochasticity. Indeed, results show that the local extinction rate was much
259 higher in bad patches, and an additional logistic regression over patch extinction during the
260 experiment showed a negative correlation between population size and extinction probability

261 ($z = -6.913, p < 0.001$). This positive relationship with time before extinction proposed by
262 Lande (1993) effectively links the carrying capacity to habitat quality. Because of this
263 instability, bad patches acted more as stepping stones between the good patches than habitats
264 harbouring persistent populations. Moreover, the small size of the populations in bad patches
265 made dispersal between the good ones more difficult. Indeed, small populations are less likely
266 to produce enough successful dispersing individuals to colonise other patches (Morel-Journel
267 et al. 2016). This is also confirmed experimentally, as another logistic regression showed that
268 empty patches had higher chances of being colonised when they were next larger populations
269 ($z = 3.796, p < 0.001$). Although the scale of fragmentation we used in this study did not prevent
270 dispersal between good patches altogether, it made it more challenging.

271 Several theoretical studies underline the importance of the scale of the fragmentation
272 of the landscape. It has to be in the same order of magnitude as the dispersal capabilities of
273 individuals to impact the invasion process (With and King 1999, With 2002, Dewhurst and
274 Lutscher 2009). Indeed, the presence of unfavourable habitat is not relevant for individuals that
275 can always easily disperse between good patches. Thus, Dewhurst and Lutscher (2009) argue
276 that fragmentation should be considered relative to individual dispersal patterns. Previous
277 experiments by Morel-Journel et al. (2016) in a similar experimental context indicate that
278 *Trichogramma* were at most able to colonise patches directly adjacent to existing populations.
279 Similarly, in our simulations, individual dispersal during a generation was limited to the
280 neighbouring patch. Therefore, individuals were not able to avoid the bad patches altogether,
281 although they were still able to get through them by forming small, unstable colonies in the bad
282 patches. Adding long distance dispersal events could modify the impact of fragmentation on
283 colonisation, as they can drastically change spread patterns across space (Johnson et al. 2006,
284 Fletcher and Westcott 2013).

285 The focus of our study – the initial establishment of an introduced population and the

286 colonisation of nearby patches – conditioned the size of the landscape studied. Indeed, we chose
287 to consider a landscape of limited size (eleven patches), which represent a section of an infinite
288 landscape with alternating good and bad patches. Similar one-dimensional landscapes have
289 been used by Shigesada et al. (1986) and Dewhirst and Lutscher (2009) to model the effects of
290 fragmentation on colonisation. Despite its small size, the landscape we focus on allowed us to
291 observe two distinct colonisation patterns in clustered landscapes: within a cluster and between
292 clusters. The first one is much easier than colonisation in fragmented landscapes, and occurs
293 even when colonisation costs are high. However, the second is more difficult and can drastically
294 limit the spread of individuals. Over larger scales, the spread pattern is therefore expected to
295 alternate between rapid colonisation of clusters, followed by much slower colonisations until
296 invaders manage to reach the next cluster. In landscapes with very low fragmentation levels,
297 the stagnation time could become overwhelming, thus effectively circumventing the invasion
298 to the clusters already colonised. This could be the case of our experimental results in clustered
299 landscapes, although the time to reach a new patch could also be greater than the duration of
300 the experiment. Other theoretical studies suggest that the dual effect of fragmentation we
301 demonstrated on one-dimensional theoretical and laboratory landscapes should persist un
302 higher dimension (With and King 1999, Roques and Chekroun 2010).

303 The effects of fragmentation, with or without habitat loss, on the dynamics of already
304 established populations, has been largely documented through empirical studies in the context
305 of conservation (Haddad et al. 2015). However in invasion biology, the subject has been mostly
306 addressed by theoretical studies, although the usage of fragmentation as a tool for the
307 management of invasion has been proposed in the past (Novinger and Rahel 2003, Alofs and
308 Fowler 2010). Our results indicate that habitat fragmentation could indeed isolate introduced
309 populations, but that it can also promote spread over larger scales. However, the outcome of
310 invasions in scattered and clustered landscapes is also highly dependent on the costs associated

311 to colonisation, either the mortality during dispersal, or the failure to reproduce after dispersal
312 because of Allee effects. This study confirms that considering the spatial distribution of
313 favourable habitat across the introduction area, and especially its interaction with population
314 dynamics is critical to assess establishment and spread probabilities. These results emphasize
315 the importance of landscape-level characteristics as an essential component of invasion success.

316

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321

322 **Author contributions**

323 T.M-J, L.M. and E.V. designed the models and experiments, T.M-J performed the simulations,
324 T.M-J and M.H. carried out the experiments and data analyses, all authors participated in the
325 writing of the manuscript.

326

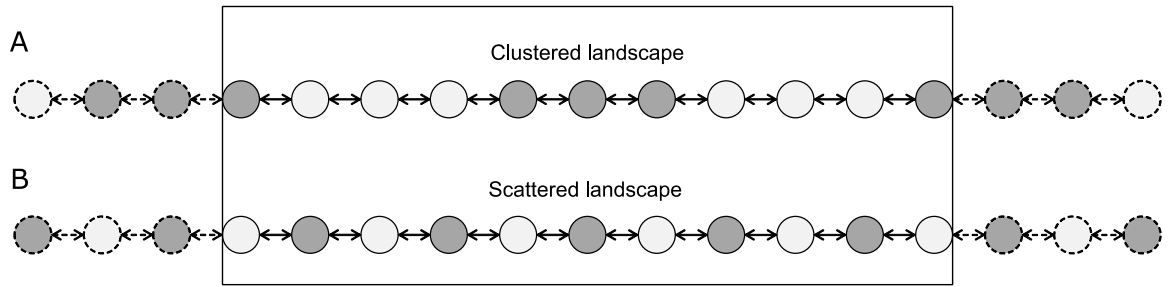
327 **Competing financial interests**

328 The authors declare no competing financial interests.

329

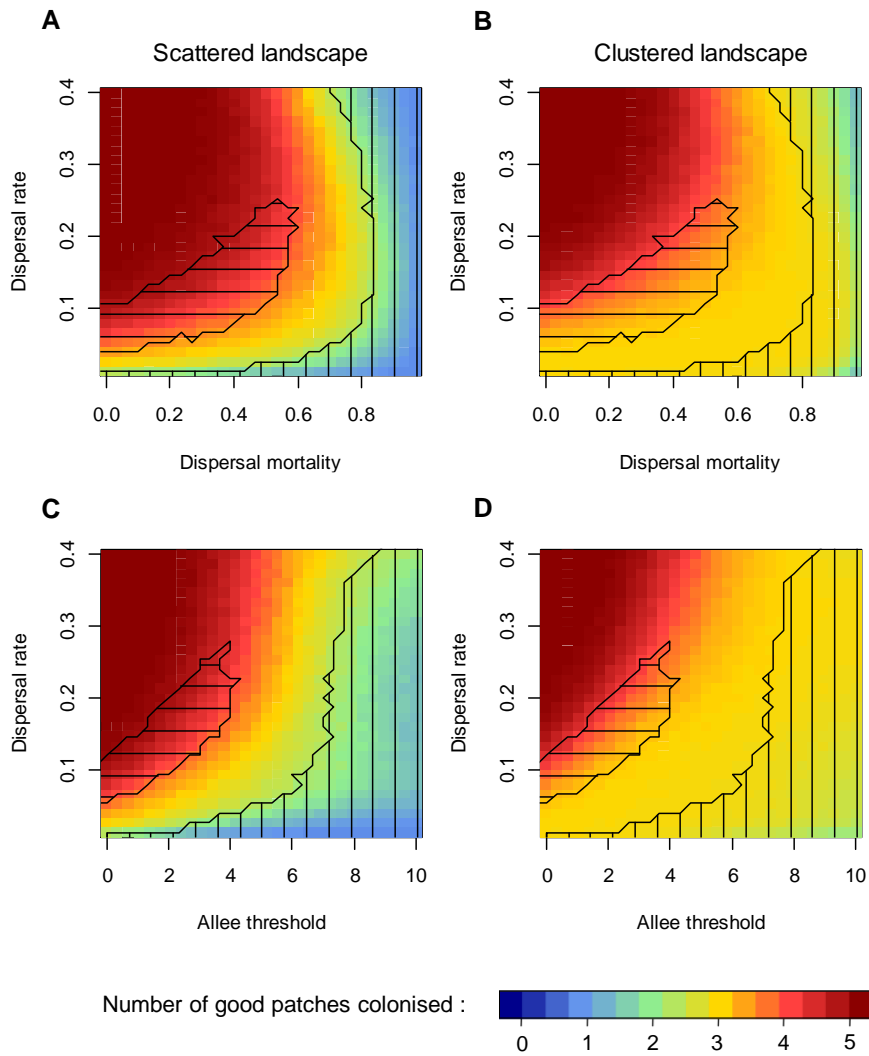
330 **Data availability**

331 The computer code to perform the simulations and the experimental data will be made available
332 on Dryad upon acceptance.

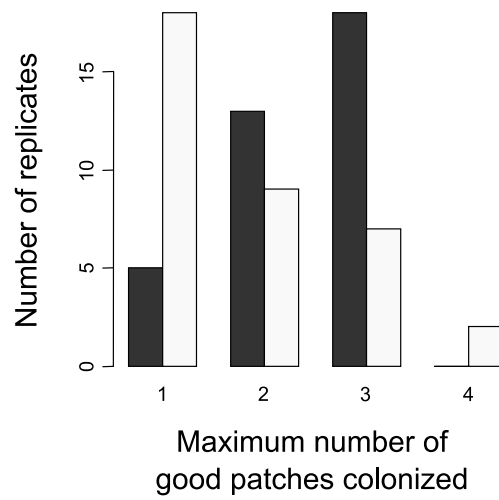


333

334 **Figure 1:** Schematic representation of the landscapes considered (A, B), and the way patches
 335 were connected in the experiment (C, D, E). Patches are represented as circles, and arrows as
 336 possible dispersal paths. The clustered (A) and scattered landscapes (B) are a part of an infinite
 337 landscape with alternating good patches (dark grey circles) and bad patches (light grey circles).
 338 Each landscape is made up of 11 patches (in the box). In the experiment, two corridors linked
 339 neighbouring patches, with no (C), one (D) or two dead-ends (D) for low, medium and high
 340 dispersal mortality respectively.



341
 342 **Figure 2:** Mean maximal number of good patches colonised (from dark blue to dark red), ten
 343 generations after introduction over 1000 simulations, for different dispersal rates and dispersal
 344 mortality levels (A, B) or Allee thresholds (C,D), in scattered (A, C) and clustered landscape
 345 (B, D). Parameter combinations for which invasions in scattered landscapes colonised on
 346 average at least 0.5 more patches than in clustered landscapes are hatched horizontally.
 347 Parameter combinations for which invasions in clustered landscapes colonised on average at
 348 least 0.5 more patches than in scattered landscapes are hatched vertically.



349
350
351
352

Figure 3: Maximum extent of the colonisation over the course of the experiment, as the number of good patches colonised, in the clustered landscape (dark bars) and the scattered landscape (light bars).

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