

**Clustered or scattered? The impact of habitat quality clustering on establishment and early spread**

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## Abstract

The match between the environmental conditions of an introduction area and the preferences of an introduced species is the first prerequisite for establishment. Yet, introduction areas are usually landscapes, i.e. heterogeneous sets of habitats that are more or less favourable to the introduced species. Because individuals are able to disperse after their introduction, the quality of the habitat surrounding the introduction site is as critical to the persistence of introduced populations as the quality of the introduction site itself. Moreover, demographic mechanisms such as Allee effects or dispersal mortality can hamper dispersal and affect spread across the landscape, in interaction with the spatial distribution of favourable habitat patches. In this study, we investigate the impact of the spatial distribution of heterogeneous quality habitats on establishment and early spread. First, we simulated introductions in one-dimensional landscapes for different dispersal rates and either dispersal mortality or Allee effects. The landscapes differed by the distribution of favourable and less favourable habitats, which were either clustered into few large aggregates of the same quality or scattered into multiple smaller ones. Second, we tested the predictions of simulations by performing experimental introductions of hymenopteran parasitoids (*Trichogramma chilonis*) in "clustered" and "scattered" microcosm landscapes. Results highlighted two impacts of the clustering of favourable habitat: by decreasing the risks of dispersal from the introduction site to unfavourable habitat early during the invasion, it increased establishment success. However, by increasing the distance between favourable habitat patches, it also hindered the subsequent spread of introduced species over larger areas.

## Introduction

Establishment is a crucial phase of biological invasions, which determines whether the introduced populations turn into self-sustaining colonies likely to spread or go extinct (Blackburn et al. 2011). The match between the characteristics of the introduced species and the environmental conditions they experience in their introduction site is a major predictor of establishment success (Shea and Chesson 2002, Moles et al. 2008), but the habitat surrounding of the introduction must also be taken into account (Melbourne et al. 2007). Introduced individuals are susceptible to disperse to the neighbouring habitats, and their environmental conditions can influence their ability to form multiple colonies in the introduction area. Dispersal early after the introduction can endanger the introduced population by reducing its size (Kean and Barlow 2000, Parlato and Armstrong 2013). It can also increase establishment success if colonisation leads to the creation of lead to the creation of a metapopulation in the introduction area. Yet, this introduction area is usually a natural landscape, made up of heterogeneous habitats (Turner et al. 2001). Colonisation and establishment can be affected by this heterogeneity, but also by the spatial distribution of these habitats of different quality (Schreiber and Lloyd-Smith 2009). This study aims at understanding the impact of the spatial distribution of heterogeneous habitat in the introduction area on the establishment and early spread of invasive species.

To do so, we considered heterogeneous landscapes made up of “rich” and “poor” habitats, respectively well and poorly matching with the invader’s characteristics. For a constant proportion of rich and poor habitat, one can define the clustering level of habitat quality. When the clustering level is increased, richer habitat is clumped in large areas separated by large areas of poor habitat. Theoretical studies identify two impacts of habitat quality clustering, at two different spatial scales. On the one hand, Schreiber and Lloyd-Smith (2009) suggest that individuals introduced in rich patches are more likely form colonies around the introduction site – and thus increase establishment probabilities – if it sits within a large cluster of rich habitat. On the other hand, several theoretical studies also suggest that scattering habitat across the landscapes reduces the mean distance between each cluster, thus increasing dispersal success (Fahrig 2003, Roques and Chekroun 2010). Simulations by Dewhurst and Lutscher (2009) indicate that aggregating resource into large and thus more isolated clusters, can prevent spread. Hence, isolating areas of favourable habitat has been proposed as a tool for the management of invasive populations (Novinger and Rahel 2003, Alofs and Fowler 2010).

The balance between these opposite effects of habitat quality distribution will likely be affected by

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demographic processes that shape colonization dynamics in heterogeneous environments. Mechanisms such as dispersal mortality or Allee effects create additional costs to dispersal that make colonisation more difficult. Dispersal mortality eliminates dispersing individuals, thus reducing the chances that some of them reach favourable habitat to colonise. On the other hand, Allee effects can bring small populations to extinction at low densities (Allee 1949, Courchamp et al. 2008), and prevent colonisation if the number of individuals dispersing to a new patch is too low (Keitt et al. 2001). By affecting colonization success, these mechanisms may exacerbate the effects of clustering. Theoretical work by Dowdall et al. (2017) showed that Allee effect interacted with spatial heterogeneity to stop invasions.

The distribution of habitat heterogeneity has been identified theoretically as a key element of landscape structure with regards to the dynamics of expanding invasive populations, and recent development of modelling framework could help better predict establishment and spread across a given landscape (Lustig et al. 2017). Yet, experimental confirmations of the impact of resource distribution on the establishment and spread of introduced populations remain scarce. Empirical studies investigated the role of spatial environmental autocorrelation, i.e. the clustering of habitat quality, on the distribution of invasive species (e.g. Manning et al. 2007, Petty et al. 2012, Moriguchi et al. 2015). Yet, these studies concern mostly a posteriori analyses of fortuitous invasions after their spread far beyond the surroundings of the introduction site, and only allow for correlative approaches. Properly testing hypotheses in invasion biology is challenging, because of the technical and ethical limitations of purposefully introducing exotic species in the wild. Microcosm experiments offer an alternative method avoiding these problems, and has been used to study invasion. Such method was used to investigate the evolution of dispersal during spread (Ochocki and Miller 2017, Weiss-Lehman et al. 2017), the role of sex-biased dispersal (Miller and Inouye 2013) or demographic stochasticity (Melbourne and Hastings 2009) on spread rates. Here, we propose to investigate the events occurring at the beginning of an invasion, at the scale of the introduction area, using similar microcosm experiments, combined with stochastic simulations.

First, we developed a simple model describing a biological invasion in a spatially explicit context. We designed heterogeneous one-dimensional landscapes with alternating poor and rich patches, according to their quality, and centred around the introduction site. Two clustering levels were considered: “scattered” landscapes alternated one rich and one poor patch, and “clustered” landscapes alternated three rich and three poor patches (Figure 1A, B). We simulated invasions in these landscapes for different dispersal rates, combined with either dispersal mortality or Allee effects. Then, we tested the predictions from the model by

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monitoring artificial introductions of the hymenopteran parasitoid *Trichogramma chilonis* in microcosms, i.e. small-scale controlled systems, especially suited to focus on specific processes (Drake and Kramer 2012). With this experimental setup, we were able to manipulate habitat distribution across the landscape, and test its impact on invasion. We created artificial landscapes with the same habitat distribution as the one used in the simulations and corresponding to either scattered or clustered landscapes. Because microcosms are highly replicable, we could initiate numerous artificial invasions in an identical environment in order to accurately estimate invasion dynamics, which are inherently very stochastic (Melbourne and Hastings 2009). Contrarily to population size assessments in the field, which are challenging and potentially imprecise for small populations, such as those just after introduction (Hayes et al. 2005), we were able to accurately follow populations dynamics from their beginning, and confront simulation and experimental results.

## Methods

### *Structure of the landscape*

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

### *Model and simulations*

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

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

1)

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

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

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

2)

where  $d_{j,t}$  is the probability that an individual disperses to one of the neighbouring patches and  $m$  accounts for dispersal mortality. Individuals can only stay in their own patch ( $|j - i| = 0$ ), or disperse to an adjacent patch ( $|j - i| = 1$ ). This limited kernel allows us to focus on short-distance dispersal, and corresponds to the dispersal behaviour also observed in the experimental setup used conjointly with the simulations. The growth phase is described by a Ricker model including an Allee effect (Brassil 2001, Courchamp et al. 2008):

$$f(x) = x e^{r(1-\frac{x}{K})(1-\frac{A}{x})}$$

3)

when  $x \geq 1$  and  $f(0) = 0$ . Here  $r$  is the per capita growth rate and  $A$  is the Allee threshold. There is no Allee effect when  $A = 0$ , a weak Allee effect when  $0 < A < 1$  and a strong Allee effect when  $A > 1$ . We added a normally distributed noise  $\varepsilon$  to the deterministic growth rate in (3) to take demographic and environmental stochasticities into account (Lande et al. 2003):

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

4)

$\sigma_\varepsilon^2$  and  $\frac{\sigma_d^2}{x}$  correspond to variability in the population growth rate respectively caused by environmental and

demographic stochasticity. As demographic stochasticity stemmed from the variability in individual fitness, its effect on the population growth rate was averaged over the whole population: if the variance in individual fitness from one individual to the other was  $\sigma_d^2$  the resulting variance at the population scale was  $\frac{\sigma_d^2}{x}$ .

The model was used to simulate introductions in the landscapes described in the previous section, for  $K_1 = 60$  and  $K_2 = 300$  to maintain the 1:5 ratio between  $K_1$  and  $K_2$ . We followed the invasions during 10 generations, for varying values of  $d_{j,t}$  (dispersal rate), and either  $A$  (Allee threshold) or  $m$  (dispersal mortality). For each of those three parameters, we selected 20 values equally distributed between 0 and 0.4 (for  $d_{j,t}$ ), 0 and 10 (for  $A$ ), 0 and 1 (for  $m$ ). Because the model is stochastic, each combination of parameters was simulated 1000 times for  $r = 1$ ,  $\sigma_e^2 = 0.1$  and  $\sigma_d^2 = 0.1$ . For each simulation, the maximal extent of the metapopulation was computed as the number of rich patches colonized outside of the introduction site. We analysed this maximum extent for each pair of dispersal rate and cost to colonisation (Allee effect or dispersal mortality) using linear models including the clustering level as an explicative variable. We compared the deviance explained by this model to the deviance of the null model to estimate the proportion of deviance explained by the clustering level (Supplementary Table 1 & 2).

### Experiment

In complement to the simulations, we performed introductions of *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae) in artificial landscapes and monitored the dynamics over ten generations. This microcosm setup aimed at recreating specifically two processes on a smaller scale: (i) local population dynamics occurring inside distinct patches and impacted by local habitat quality (ii) dispersal processes linking the patches and allowing a potential progressive colonization of the landscape. To this end each microcosm was made up of a set of 11 patches (each is a plastic tube of height: 100 mm and diameter: 50 mm), linked to one another by corridors (plastic pipes of length: 400 mm and diameter: 5 mm). The whole experimental system was maintained in constant temperature and light conditions, with a 16 hours daylight (25°C) / 8 hours dark (20°C) cycle, and 70% humidity.

*T. chilonis* is a minute parasitoid wasp (size < 1 mm), whose larva developed in eggs of the Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) for this experiment. *E. kuehniella* eggs were irradiated prior to their usage, which prevented the development of the host while the parasitoid larvae could develop. Each generation lasted nine days, including two days of adult life and seven days of

larval development inside the host. During the adult phase, food was provided ad libitum in the form of honey drops. Individuals dispersed and reproduced for 48 hours, after which they were manually removed from the experiment to maintain non-overlapping generations. While individuals were able to move freely between patches by walking through pipes, the dispersal rates in this experimental system remained low. Previous experiments (Morel-Journel et al. 2016) in similar conditions showed that most individuals remained in their natal patch, and no individual was ever found further than one patch away from its natal patch. Because dispersal events were rare, the population dynamics in each patch remained largely independent. The experiment was monitored by counting the number of parasitized eggs at each generation, during the larval phase. The larvae developing within the eggs would eventually turn dark because of the chitinisation of the parasitoid pupae (Reay-Jones et al. 2006). As only one individual is usually able to fully develop from one host (Suzuki et al. 1984), the number of dark eggs was considered a reliable proxy of the number of adults in the next generation. Population sizes were estimated by counting the number of parasitized eggs in each patch at each generation.

To create differences in habitat quality in order to create rich and poor patches, we manipulated the number of hosts available for parasitism. The carrying capacities in the experiment were controlled by the number of hosts available. Rich patches were provided with approx. 450 eggs at each generation, as previous experiments by Vercken et al. (2013) indicate that *T.chilonis* populations would reach carrying capacities around 300 individuals in these conditions. The poor patches were provided with approx. 90 eggs to maintain a 1:5 ratio between  $K_1$  and  $K_2$ , comparable to what was investigated with the model.

We set up a 2 x 3 factorial design for the experiment, with two quality clustering levels and three levels of dispersal mortality. Patches of rich and poor quality were connected to form either clustered (Figure 1A) or scattered landscapes (Figure 1B). We only considered one type of cost to colonization to increase the number of experimental replicates and have more statistical power in the analyses. Dispersal mortality was chosen over demographic Allee effects, which is more species-dependent and less widespread in empirical data (Kramer et al. 2009, Gregory et al. 2010), despite a large use in theoretical studies. We manipulated dispersal mortality by adding optional dead-end exits to the pipes connecting adjacent patches. Those dead-ends made successful dispersal to neighbouring patches less likely, as individuals stayed in these dead ends without finding the next patch (results not shown). Two adjacent patches were thus connected with either (i) two regular pipes for low dispersal mortality, (ii) one regular and one pipe with a dead-end exit for medium dispersal mortality, (iii) two pipes with dead-end exits for high dispersal mortality (Figure 1C, D, E). Each



factorial combination was replicated twelve times, for a total of 72 experimental landscapes. Each replicate was initiated with the introduction of five mated females in the central patch (Figure 1A, B).

First, we looked to characterize the impact of patch quality on persistence and colonisation. We computed the mean extinction rates of rich and poor patches for each replicate and compared them using a paired Wilcoxon test. Since patch quality was linked to their carrying capacity, we also tested the relationship between the size of a population and i) its extinction risks, ii) the probability of colonisation of adjacent patches. Both those probabilities were analysed using a logistic regression. Second, we characterized colonisation at the landscape level. As we expected to observe different effects of the distribution of rich and poor habitat on early invasion at two different spatial scales, we characterized (i) the surroundings of the introduction site as the two rich patches closest to the introduction site (i.e. those directly linked to the introduction site in the clustered landscape or those one poor patch away from the introduction site in the scattered landscape) and (ii) the rest of the landscape as the two rich patches furthest from the introduction site. We computed the surroundings and landscape occupancy rates as the proportion of replicates in which at least one rich patch was colonised, in the surroundings and the rest of the landscape respectively. The surroundings occupancy rate was analysed with a binomial general linear mixed model, with the experimental block as a random effect. Model averaging was performed over the candidate models according to their  $AIC_C$  (Grueber et al. 2011): (i) without any fixed factor, (ii) with dispersal mortality as a factor, (iii) with landscape clustering as a factor, (iv) with the additive effect of both factors (Supplementary Table 3). As there were very few colonisations in the rest of the landscape, the landscape occupancy rate was analysed with Fisher's exact tests.

## Results

In accordance with our predictions, we observed an overall positive relationship between colonisation and the dispersal rate, and a negative relationship between colonisation and the mechanism creating additional costs to colonisation, i.e. Allee effects or dispersal mortality (Figure 2). The impacts of the two mechanisms on colonisation were similar. We found parameter combinations for which the clustering level explained more than 15% of the deviance in the simulated data. For high colonisation costs and very low dispersal rates, populations in clustered landscapes performed better than those in scattered landscapes. The first colonised the surroundings of the introduction site and created metapopulations in their local cluster, while the second colonised only in their introduction site. For intermediate dispersal rates and low

colonisation costs, all populations managed to colonise other rich patch and form metapopulations. However, populations in clustered landscapes achieved lower colonization than those in scattered landscapes: the first only colonised the surroundings of the introduction site while the others managed to colonise the rest of the landscape.

Experimental results confirmed the impact of habitat quality on local population dynamics, as the poor patches had a significantly higher extinction rate than the rich ones (paired Wilcoxon test,  $V = 706.5$ ,  $p < 0.001$ ). Logistic regressions did not only confirm that small populations had higher extinction risks ( $z = 6.913$ ,  $p < 0.001$ ), but also that that empty patches had higher chances of being colonised when they were adjacent to larger populations ( $z = 3.796$ ,  $p < 0.001$ ).

We also observed clear patterns concerning the colonisation (Figure 3). We assessed the occupancy rate of the rich patches surrounding the introduction site, and in the rest of the landscape separately. The clustering level affected positively the surroundings occupancy rate (Wald test,  $z = -4.282$ ,  $p < 0.001$ ), but negatively the landscape occupancy rate (Fisher's exact test,  $p = 0.025$ ). Thus, populations introduced in clustered landscapes managed to form metapopulations by colonising patches in the surroundings much more often than those introduced in scattered landscapes, but did not manage to successfully colonise the rich patches outside of their local cluster. Finally, we identified a negative impact of dispersal mortality on the surroundings occupancy rate (Wald test,  $z = -2.243$ ,  $p = 0.025$ ), but not on the landscape occupancy rate (Fisher's exact test,  $p = 0.865$ ).

## Discussion

Simulation and experiment results confirm the twofold impact of the spatial distribution of habitat quality across the landscape on invasion success, depending on the costs associated with dispersal. Breaking apart favourable habitat in small fragments in the landscape reduced the formation of colonies close to the introduction site, while facilitating dispersal over larger scales. When colonisation was not impaired (when the costs of dispersal were low or inexistent), simulation results indicated that clustering of favourable habitat could slow down colonisation at larger scales by increasing the mean distance between clusters of rich habitat. These results were consistent with the patterns observed during the experiment. Indeed, the only recorded colonisations of the furthest patches from the introduction site occurred in scattered landscapes.

They also concur with earlier theoretical work on the positive effect of rich habitat scattering on invasive spread (With 2002, Fahrig 2003). Indeed, scattered habitat can provide stepping stones, which

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increase connectivity within a landscape (Schippers et al. 2008, Saura et al. 2014). When the costs associated with dispersal were higher, habitat clustering became favourable to colonisation. Dispersal mortality and Allee effects increased the minimal number of dispersing individuals necessary to successfully colonise patches, respectively by eliminating some of them during dispersal and by raising the minimal initial population size necessary to ensure colonisation. The presence of poor patches, harbouring fewer individuals, around the introduction site in scattered landscapes, did not prevent colonisation of other rich patches altogether, although it made it more difficult. This conclusion is supported by the lower colonisation rate of the surroundings of the introduction site observed during the experiments in the scattered landscapes.

Dispersal mortality risks and Allee effects were considered separately during the simulations, and previous results by Morel-Journel et al. (2016) concluded that *T. chilonis* suffered from no demographic Allee effect in this particular experimental setting. However, the two mechanisms can also influence each other. Using individual-based models and field experiments on the invasive moth *Lymantria dispar*, Walter et al. (2016) showed that dispersal mortality could increase the Allee threshold of populations. Indeed, their results indicate that deaths during dispersal across heterogeneous landscapes significantly increase the minimal number of individuals necessary to create a self-sufficient population. While we consider here only Allee effects at the demographic level, the Allee threshold in their study is the result of an underlying mate-finding failure documented in *L. dispar*.

In previous theoretical studies on the subject, poor patches were characterized by a negative population growth rate (Lutscher et al. 2006, e.g. Dewhurst and Lutscher 2009) and so acted like barriers to dispersal. In our study, heterogeneity was created by the carrying capacity. Therefore, poor patches could harbour populations, although smaller than those in rich patches, thus more prone to stochastic extinction. Indeed, results confirmed that the extinction probability of populations in the experiment was negatively correlated with their size. This relationship is consistent with the positive impact carrying capacity on time before extinction proposed by Lande (1993). Poor patches harboured populations with higher extinction risks, but could still be used as stepping stones between the rich patches. Yet, the experiment showed that patches neighbouring small populations were less likely to be colonised. Indeed, small populations are less likely to produce enough successful dispersing individuals to colonise other patches (Morel-Journel et al. 2016). Although the scale of habitat clustering we used in this study did not prevent dispersal between rich patches altogether, it made it more challenging.

Several theoretical studies underline the importance of the scale of habitat heterogeneity. It has to

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be in the same order of magnitude as the dispersal capabilities of individuals to impact the invasion process (With and King 1999, With 2002, Dewhirst and Lutscher 2009). Indeed, the presence of less habitat is not relevant for individuals that can always easily disperse between rich patches. Thus, Dewhirst and Lutscher (2009) argue that the structure of habitat quality should be considered relative to individual dispersal patterns. In our simulations and our experimental setup, individuals were at most able to colonise patches directly adjacent to existing populations. Therefore, they were not able to avoid the poor patches altogether, although they were still able to get through them by forming small, unstable colonies in the poor patches. Adding long distance dispersal events could modify the rate of colonisation, as they can drastically change spread patterns across space (Johnson et al. 2006, Fletcher and Westcott 2013).

In nature, scattered distribution of favourable habitat is often the result of habitat loss and fragmentation, and is characteristic of disturbed landscapes. Empirical studies suggest that invasive species are often seen to thrive on this type of landscape (Suarez et al. 1998, Holway et al. 2002, Marvier et al. 2004). Indeed, a one-time disturbance can profoundly destabilize a community of native species highly adapted to their pre-disturbance environment, and promote the invasion of a more generalist exotic species (Marvier et al. 2004). This community-level effect acts separately from the mechanisms considered in this study, which act on introduced populations independently from the structure of the native community. While fragmentation can bring introduced populations to extinction, our results also suggest that the ones that establish spread more easily in such fragmented and disturbed landscapes. This effect could add up with the increased invasibility of disturbed native community, and increase further the risks of large-scale invasions in the context of fragmentation and habitat loss.

The focus of our study – the initial establishment of an introduced population and the colonisation of nearby patches – conditioned the size of the landscape studied. Indeed, we chose to consider a landscape of limited size (eleven patches), which represent a section of an infinite landscape with alternating rich and poor patches. Similar one-dimensional landscapes have been used by Shigesada et al. (1986) and Dewhirst and Lutscher (2009) to model the effects of habitat distribution on colonisation. Despite its small size, the landscape we focus on allowed us to observe two distinct colonisation patterns in clustered landscapes: within a cluster and between clusters. The first one is much easier than colonisation in scattered landscapes, and occurs even when colonisation costs are high. However, the second is more difficult and can drastically limit the spread of individuals. Over larger scales, the spread pattern is therefore expected to alternate between rapid colonisation of clusters, followed by much slower colonisations until invaders manage to reach

the next cluster. In landscapes with very high clustering levels, the stagnation time could become overwhelming, thus effectively circumventing the invasion to the clusters already colonised. Theoretical studies have showed that a high enough clustering level could actually pin the invasion front if the invader suffers from Allee effects, even if the difference between the rich and the poor patches is small (Dowdall et al. 2017). Besides, invasions can also be pinned for lower clustering levels for greater heterogeneity between the patches (Maciel and Lutscher 2015), suggesting that invasion pinning depends on the interaction between the two parameters. Other theoretical studies suggest that the effect we demonstrated on one-dimensional theoretical and laboratory landscapes should persist in higher dimensional spaces (With and King 1999, Roques and Chekroun 2010).

In this study, we provide an empirical test of the role of the spatial distribution of habitat quality on establishment and spread. Our results confirm the body of theoretical studies on the subject, and the correlations recorded in empirical studies. We show that although scattering favourable habitat could isolate introduced populations, it can also promote spread over larger scales. However, the outcome of invasions in scattered and clustered landscapes is also highly dependent on the costs associated to colonisation, either the mortality during dispersal, or the failure to reproduce after dispersal because of Allee effects. This study confirms that considering the spatial distribution of favourable habitat across the introduction area, and especially its interaction with population dynamics is critical to assess establishment and spread probabilities. These results emphasize the importance of landscape-level characteristics as an essential component of invasion success.

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#### **Author contributions**

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

#### **Competing financial interests**

The authors declare no competing financial interests.

#### **Data availability**

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

#### **References**

- Allee, W. C. 1949. *Principles of Animal Ecology*. - Saunders.
- Alofs, K. M. and Fowler, N. L. 2010. Habitat fragmentation caused by woody plant encroachment inhibits the spread of an invasive grass. - *J. Appl. Ecol.* 47: 338–347.
- Blackburn, T. M. et al. 2011. A proposed unified framework for biological invasions. - *Trends Ecol. Evol.* 26: 333–339.
- Brassil, C. E. 2001. Mean time to extinction of a metapopulation with an Allee effect. - *Ecol. Model.* 143: 9–16.
- Courchamp, F. et al. 2008. *Allee Effects in Ecology and Conservation*. - Oxford University Press.
- Dewhurst, S. and Lutscher, F. 2009. Dispersal in heterogeneous habitats: thresholds, spatial scales, and approximate rates of spread. - *Ecology* 90: 1338–1345.
- Dowdall, J. et al. 2017. Invasion pinning in a periodically fragmented habitat. - *J. Math. Biol.*: 1–24.
- Drake, J. M. and Kramer, A. M. 2012. Mechanistic analogy: How microcosms explain nature. - *Theor. Ecol.* 5: 433–444.
- Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. - *Annu. Rev. Ecol. Evol. Syst.* 34: 487–515.
- Fletcher, C. S. and Westcott, D. A. 2013. Dispersal and the design of effective management strategies for plant invasions: matching scales for success. - *Ecol. Appl.* 23: 1881–1892.
- Gregory, S. D. et al. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. - *Ecology* 91: 2151–2161.
- Grueber, C. E. et al. 2011. Multimodel inference in ecology and evolution: challenges and solutions. - *J. Evol. Biol.* 24: 699–711.
- Holway, D. A. et al. 2002. Role of Abiotic Factors in Governing Susceptibility to Invasion: A Test with Argentine Ants. - *Ecology* 83: 1610.
- Johnson, D. M. et al. 2006. Allee effects and pulsed invasion by the gypsy moth. - *Nature* 444: 361–363.
- Keitt, T. H. et al. 2001. Allee effects, invasion pinning, and species' borders. - *Am. Nat.* 157: 203–216.
- Kramer, A. M. et al. 2009. The evidence for Allee effects. - *Popul. Ecol.* 51: 341–354.
- Lande, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. - *Am. Nat.* 142: 911–927.

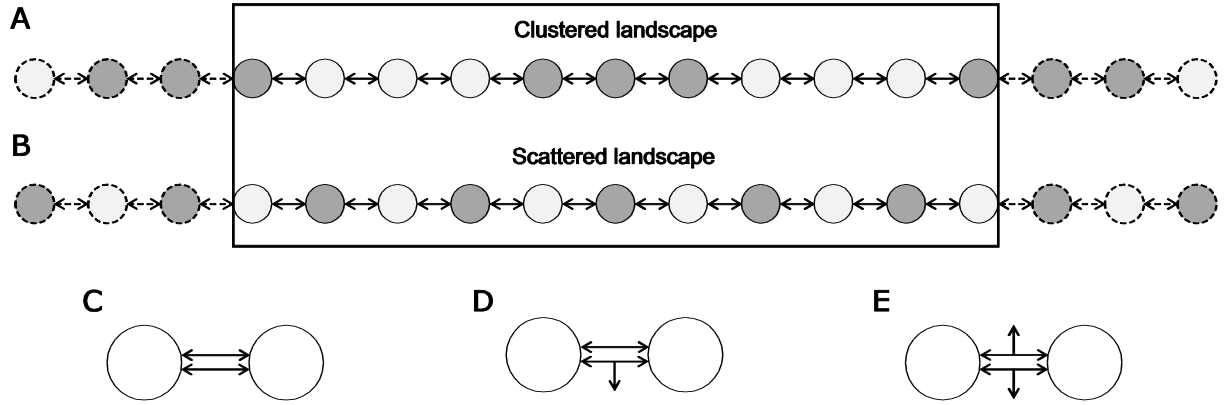
- Accepted Article
- Lande, R. et al. 2003. Stochastic Population Dynamics in Ecology and Conservation. - Oxford University Press.
- Lustig, A. et al. 2017. A modeling framework for the establishment and spread of invasive species in heterogeneous environments. - *Ecol. Evol.* 7: 8338–8348.
- Lutscher, F. et al. 2006. Effects of Heterogeneity on Spread and Persistence in Rivers. - *Bull. Math. Biol.* 68: 2129–2160.
- Maciel, G. A. and Lutscher, F. 2015. Allee effects and population spread in patchy landscapes. - *J. Biol. Dyn.* 9: 109–123.
- Manning, P. et al. 2007. Spatial heterogeneity in the determinants of woody plant invasion of lowland heath. - *Appl. Veg. Sci.* 10: 65–72.
- Marvier, M. et al. 2004. Habitat Destruction, Fragmentation, and Disturbance Promote Invasion by Habitat Generalists in a Multispecies Metapopulation. - *Risk Anal.* 24: 869–878.
- Melbourne, B. A. and Hastings, A. 2009. Highly variable spread rates in replicated biological invasions: Fundamental limits to predictability. - *Science* 325: 1536–1539.
- Miller, T. E. X. and Inouye, B. D. 2013. Sex and stochasticity affect range expansion of experimental invasions. - *Ecol. Lett.* 16: 354–361.
- Moles, A. T. et al. 2008. A new framework for predicting invasive plant species. - *J. Ecol.* 96: 13–17.
- Morel-Journel, T. et al. 2016. The highs and lows of dispersal: How connectivity and initial population size jointly shape establishment dynamics in discrete landscapes. - *Oikos* 125: 769–777.
- Moriguchi, S. et al. 2015. Estimating colonization and invasion risk maps for *Linepithema humile*, in Japan. - *J. Asia-Pac. Entomol.* 18: 343–350.
- Novinger, D. C. and Rahel, F. J. 2003. Isolation Management with Artificial Barriers as a Conservation Strategy for Cutthroat Trout in Headwater Streams. - *Conserv. Biol.* 17: 772–781.
- Ochocki, B. M. and Miller, T. E. X. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. - *Nat. Commun.* in press.
- Petty, A. M. et al. 2012. Inferring habitat suitability and spread patterns from large-scale distributions of an exotic invasive pasture grass in north Australia. - *J. Appl. Ecol.* 49: 742–752.
- Reay-Jones, F. p. f. et al. 2006. Functional response of *Trichogramma chilonis* to *Galleria mellonella* and *Chilo sacchariphagus* eggs. - *Entomol. Exp. Appl.* 118: 229–236.
- Roques, L. and Chekroun, M. D. 2010. Does reaction-diffusion support the duality of fragmentation effect? - *Ecol. Complex.* 7: 100–106.
- Saura, S. et al. 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. - *J. Appl. Ecol.* 51: 171–182.
- Schippers, P. et al. 2008. Sacrificing patches for linear habitat elements enhances metapopulation performance of woodland birds in fragmented landscapes. - *Landsc. Ecol.* 24: 1123–1133.
- Schreiber, S. J. and Lloyd-Smith, J. O. 2009. Invasion dynamics in spatially heterogeneous environments. - *Am. Nat.* 174: 490–505.
- Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. - *Trends Ecol. Evol.* 17: 170–176.

- Accepted Article
- Shigesada, N. et al. 1986. Traveling periodic waves in heterogeneous environments. - *Theor. Popul. Biol.* 30: 143–160.
- Suarez, A. V. et al. 1998. Effects of Fragmentation and Invasion on Native Ant Communities in Coastal Southern California. - *Ecology* 79: 2041–2056.
- Suzuki, Y. et al. 1984. Sex allocation and effects of superparasitism on secondary sex ratios in the gregarious parasitoid, *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). - *Anim. Behav.* 32: 478–484.
- Turner, M. G. et al. 2001. *Landscape Ecology in Theory and Practice*. - Springer-Verlag.
- Vercken, E. et al. 2013. Time-lag in extinction dynamics in experimental populations: evidence for a genetic Allee effect? - *J. Anim. Ecol.* 82: 621–631.
- Walter, J. A. et al. 2016. Invasion in patchy landscapes is affected by dispersal mortality and mate-finding failure. - *Ecology* 97: 3389–3401.
- Weiss-Lehman, C. et al. 2017. Rapid trait evolution drives increased speed and variance in experimental range expansions. - *Nat. Commun.* 8: 14303.
- With, K. A. 2002. The Landscape Ecology of Invasive Spread. - *Conserv. Biol.* 16: 1192–1203.
- With, K. A. and King, A. W. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. - *Landsc. Ecol.* 14: 73–82.

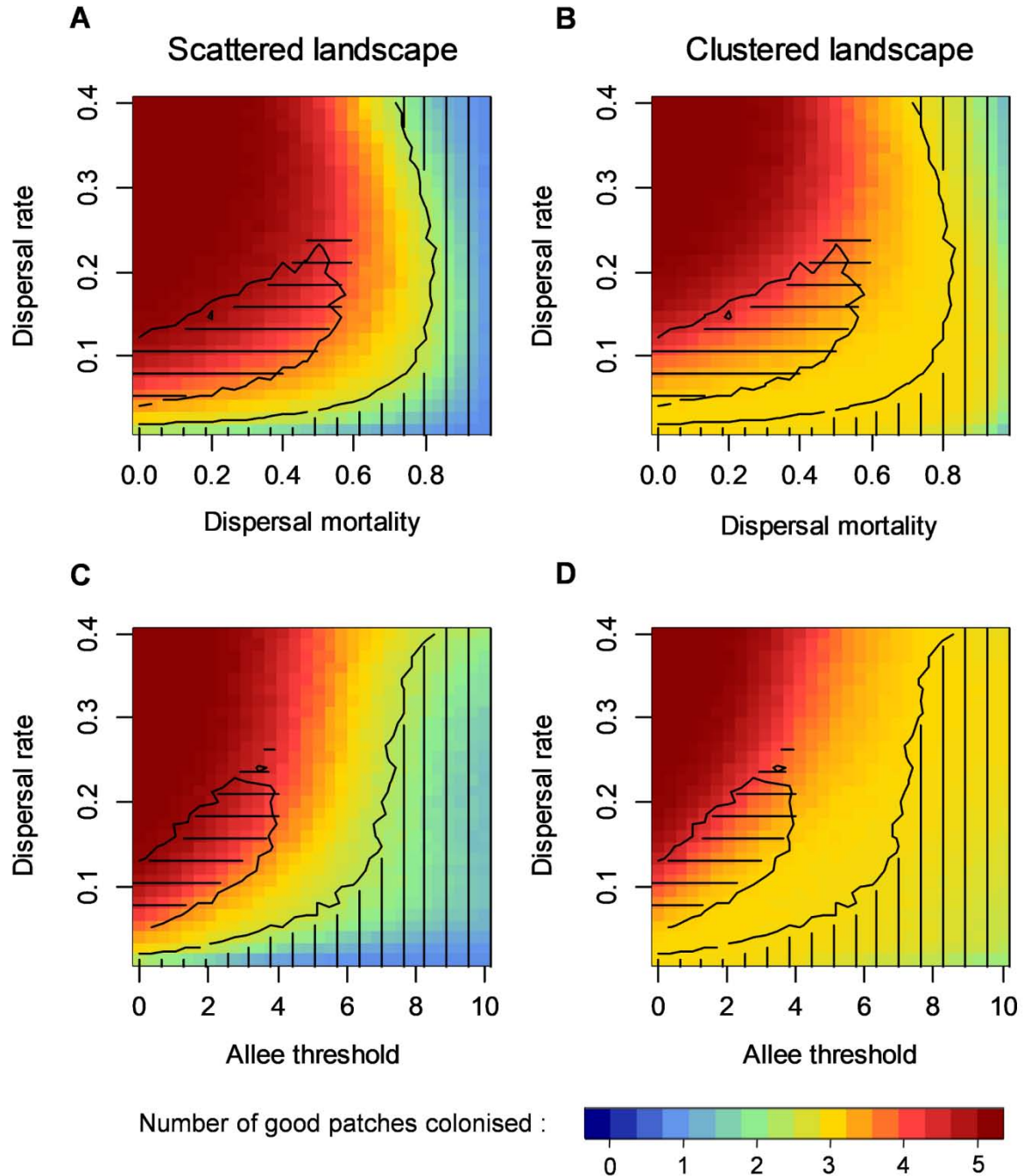


**Figure Legends**

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



**Figure 2:** Mean maximal number of rich patches colonised (from dark blue to dark red), ten generations after introduction over 1000 simulations, for different dispersal rates and dispersal mortality levels (A,B) or Allee thresholds (C,D), in scattered (A, C) and clustered landscape (B, D). Scenarios where landscape more than 15% of the variance in the simulated data was explained by the landscape type were hatched (i) vertically if more patches were colonized in scattered landscapes (ii) horizontally if more patches were colonized in clustered landscapes.



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

