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The highs and lows of dispersal: how connectivity and initial population size jointly shape establishment dynamics in discrete landscapes

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Identifying the main factors driving introduced populations to establishment is a major challenge of invasion biology. Due to their small initial size, introduced populations are most vulnerable to extinction because of demographic stochasticity or Allee effects. While an increase in initial population size is known to increase establishment success, much remains to be understood regarding its interplay with connectivity in spatially structured environments. In order to better understand how demographic mechanisms interact at such spatial scale, we developed a stochastic model of population dynamics in discrete space to investigate the effect of connectivity and initial population size on establishment. The predictions derived from the model were then tested using experimental introductions of an insect parasitoid (*Trichogramma chilonis*) in spatially structured laboratory microcosms. Both theoretical and experimental results demonstrated that the connectivity of the introduction site had 1) a deleterious effect in the first generation when the introduced population was small and 2) a beneficial impact brought about by metapopulation effects in the subsequent generations. Interestingly, populations displayed a weakly pushed invasion pattern promoting early establishment, which was mainly underpinned by dispersal stochasticity and the discrete nature of the landscape. These results shed light on the critical influence of landscape connectivity on establishment dynamics.

Providing reliable predictors of whether or not introduced individuals are able to persist in their novel environments is a crucial challenge for ecologists, with direct consequences for the management of invasive pests (Williamson and Fitter 1996), endangered species (Noël et al. 2011) or biological control agents (Freckleton 2000). Theoretical population biology (Ebenhard 1991), as well as correlative data related to introductions in nature (Hayes and Barry 2008), point towards the number of introduced individuals being the main factor important for population persistence (Simberloff 2009). However, beyond the raw number of individuals, their distribution in time and space should strongly impact their persistence (Drury et al. 2007, Garnier et al. 2012). By affecting individual dispersal, connectivity within the introduction area is expected to shape variations in population density. Understanding the effects of initial population size, connectivity, and their interaction is therefore essential to predict establishment dynamics. Throughout this study, we refer to 'establishment' as the persistence of introduced individuals anywhere within this introduction area.

Propagule size, which sets initial population size, is strongly correlated with establishment (Simberloff 2009). Indeed, small introduced populations tend to experience significantly increased extinction risks because of two non exclusive demographic mechanisms: 1) demographic stochasticity and 2) Allee effects (Fauvergue et al. 2012). Demographic stochasticity refers to the increase in variability of growth rates experienced by a population when it is small, as realized individual fecundities and mortalities tend to average out only in large populations (Lande 1993). A small population will thus be more likely to stochastically experience especially small growth rates, which might cause its extinction if the mean growth rate of the population is low enough. Allee effects correspond to decreases in the mean fitness of individuals at lower densities because of fewer beneficial interactions between individuals when they become scarce (Courchamp et al. 2008). It can be caused by numerous biological mechanisms, the most common one being failure to find mates. If the Allee effect is strong, one can define a threshold in population size, under which population growth rate is negative and the population is driven to extinction (Wang and Kot 2001).

The spatial repartition of individuals in the introduction area also plays a key role in their establishment success (Drury et al. 2007, Garnier et al. 2012). Using individual based models, Kanarek et al. (2013) showed that both the spatial distribution of individuals at introduction and their subsequent movements in the introduction area influence establishment. Introduction areas are usually not homogeneous in space, and can be seen as landscapes, i.e. a spatial mosaic of heterogeneous habitats which are more or less suited to the studied species. Connectivity is classically defined as the degree to which the landscape facilitates or impedes movement among habitats (Taylor et al. 1993). In this study, we especially considered connectivity as the extent to which landscape features let individuals disperse between patches. Depending on the species considered, those landscape features can affect their propensity to migrate, and thus modify actual dispersal rates between patches (Calabrese and Fagan 2004). On the one hand, the dispersal pattern of some species is heavily influenced by biological processes, like Allee effect avoidance (Heg et al. 2008) or quorum sensing (Pratt et al. 2002), with little impact of the landscape. On the other hand, when individuals move more randomly, dispersal patterns are strongly influenced by landscape characteristics (Jonsen and Taylor 2000). This latter type of dispersal was considered in this study, as we hypothesized that connectivity directly affected emigration rates.

While primary colonization depends on initial population size, subsequent colonizations (i.e. successful dispersal to other habitat patches in the landscape) depend on the number of dispersing individuals in the following generations. In this study, we investigated establishment in the surroundings of the introduction site, thus only short distance dispersal was considered. As connectivity increases emigration from the introduction site, its impact on establishment is thus twofold. It facilitates the formation of a metapopulation, which can increase the persistence of local populations through dynamics of extinction and recolonization (Hanski and Gaggiotti 2004) and other mechanisms such as the rescue effect (Brown and Kodric-Brown 1977). However, by increasing dispersal, connectivity also decreases individual density which can accentuate demographic stochasticity and Allee effects (Drury et al. 2007, Kanarek et al. 2013). Early emigration from a small introduced population slows down its growth (Kean and Barlow 2000), so that high connectivity of the introduction site might further weaken the initial population and increase establishment failure (Parlato and Armstrong 2013). Therefore, the consequences of connectivity on the establishment of introduced populations following introduction are complex. It may not only increase local population persistence by bringing about metapopulation effects, but also decrease it by lowering local population sizes.

Moreover, the dispersal patterns subsequent to introduction can also influence establishment. Stokes (1976) distinguish “pulled” and “pushed” invasions, which are respectively driven by the dynamics of the smaller populations on the edge, or by those of the large populations in the core of the population. Pushed invasions can be brought about by various mechanisms affecting the growth or dispersal of populations on the front edge (Bonnefon et al. 2014), the most classic one being the Allee effect (Lewis and Kareiva 1993, Roques et al. 2012). While pushed fronts were initially considered in continuous space, they can also exist in a discrete space, such as the landscape of patches considered in this study. Indeed, Panja (2004) identified “weakly pushed” fronts, whose propagation speed is driven by the core of the metapopulation. The weakly pushed nature of the front is especially relevant when populations are small, for example because of small values of carrying capacity. As they limit dispersal, pushed invasion patterns can have a positive effect on population persistence (Veit and Lewis 1996, Roques et al. 2012), while pulled invasion patterns would tend to magnify the deleterious effects of connectivity by promoting dispersal from small populations.

This study aims to answer the following questions: does connectivity of the introduction site influence establishment? Does this influence vary with the size of the introduced population? While we assumed that larger introduced populations were more likely to establish, we expected connectivity to increase colonization opportunities and affect establishment in two ways: on the one hand positively, by speeding up invasion and promoting the formation of a metapopulation, and on the other hand negatively by increasing early emigration from the introduction site and revealing potential deleterious mechanisms affecting small populations. Previous work on the stability of established populations investigated their persistence compared to isolated populations and depending on the occupancy of other patches (Hanski and Gaggiotti 2004). This study addresses similar questions, but in the non-equilibrium context of the first steps of invasion, at the onset of the formation of the metapopulation itself. To address such questions, we first developed a simple model describing invasion in a spatial context. Through simulations, we investigated the consequences of Allee effects and demographic stochasticity on establishment on different connectivity levels at the introduction site. We also studied their impact on the dispersal pattern and its influence on establishment. Then, we experimentally tested the model predictions. Artificial introductions were monitored for two initial population sizes crossed with two levels of connectivity at the introduction site in one-dimensional discrete experimental landscapes of *Trichogramma chilonis*, a hymenopteran parasitoid. Properties of the experimental invasion patterns were also characterized, and the main causes underpinning them were examined. To our knowledge, this study brings the first experimental evidence of joint effects of initial population size and connectivity of the introduction site on establishment.

Material and methods

Model

We developed a simple discrete-time model of population dynamics in an one dimensional discrete stepping-stone landscape W:

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

with $N_{j,t}$ the population size at generation t and location j in the landscape W. As $N_{j,t}$ represents the number of individuals, its value is systematically truncated to the nearest integer and the population is considered extinct when $N_{j,t} < 1$. This model splits each generation into two successive phases: 1) a dispersal phase associated with the dispersal kernel $M(i, j)$ describing the probability that an individual at location j migrates to location i, 2) a growth phase, with f a function describing the growth of the population at location i after dispersal.

At each generation, individuals can either stay in their current patch or disperse to one of the neighbouring patches with an equal probability in each direction. The probability that an individual disperses from patch j to patch i depends on their distance:

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

where $d_{j,t}$ is the probability that an individual disperses from patch j to one of the neighbouring patches and k_j the number of patches neighbouring patch j. The value of k_j for the introduction site was either 0, 1 or 2, and $k_j = 2$ for all the other patches. This dispersal probability depends on the population size just before dispersal $N_{j,t}$ (Altwegg et al. 2013):

$$d_{j,t}=d_{DI}\left(\frac{N_{j,t}}{K}\right)^{g} \tag{3}$$

where d_{DI} is the density-independent dispersal probability, K is the environment carrying capacity, and g a density-dependence parameter. When $g = 0$, dispersal does not depend on density, $g > 0$ describes positive density-dependence, i.e. individuals are less likely to disperse in small populations, and $g < 0$ describes negative density-dependence, i.e. individuals are more likely to disperse in small populations.

Population growth is assumed to follow a Ricker model, modified to include a potential demographic Allee effect (Brassil 2001):

$$f(x)=x\,e^{r\left(1-\frac{x}{K}\right)\left(1-\frac{A}{x}\right)} \tag{4}$$

where r is the per capital 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 $A > 1$. A normally distributed noise ε is added to the deterministic growth rate in Eq. 5 to take demographic and environmental stochasticities into account (Lande et al. 2003):

$$f(x)=x\,e^{r(1-x/K)(1-A/x)+\varepsilon},\ \varepsilon+N\left(0,\sigma_e^2+\sigma_d^2/x\right) \tag{5}$$

σ^2_e and σ^2_d / x represent the variability in the population growth rate caused respectively by environmental and demographic stochasticity. As σ^2_d stems from the variability in individual fitness, it is averaged over the population size at the population level (Lande et al. 2003). Environmental stochasticity was entirely uncorrelated between patches. This would represent environmental variations at a small spatial scale that do not interfere with key features of metapopulation dynamics such as rescue effects.

Simulations

Simulations of this model were performed with the R software (<www.r-project.org>). Firstly, we simulated the combined effects of initial population size and connectivity level at the introduction site on the establishment of introduced populations. As connectivity corresponds to the permeability of landscape to dispersal, it refers here to the number of dispersal opportunities from the introduction site, as well as the number of directions in which emigrating individuals could disperse. Individuals introduced in the one-dimensional landscape 1) could not disperse to other patches (Fig. 1A), 2) could disperse only on one side of the introduction site (Fig. 1B) or 3) could disperse on both sides of the introduction site (Fig. 1C). There was no dispersing individual in case 1) and the introduction site was similar to an isolated patch. In case 2), only the individuals dispersing on the right-hand side of the introduction site according to the dispersal kernel M (i, j) were counted as dispersing individuals. By varying parameter values in Eq. 5, we tested the influence of demographic stochasticity alone, both demographic and environmental stochasticity, or demographic stochasticity in presence of a strong Allee effect. Each scenario was simulated 1000 times for different combinations of values for initial population size (between one and 30 individuals) and the three connectivity levels described above, with $r = 0.3$, $K = 300$, $d_{DI} = 0.3$, $g = 0$ and $\sigma^2_d = 0.1$. Establishment rate was estimated as the proportion of non-extinct simulated populations 10 generations after introduction.

We also simulated the effects of 1) demographic Allee effects, 2) density-dependent dispersal and 3) stochastic dispersal separately on the invasion pattern. We simulated 10 generations after a single introduction in a linear discrete landscape. Scenarios 1) and 2) were simulated by varying values of the Allee threshold A, and density-dependence parameter g, to generate respectively Allee effects and positive or negative density-dependent dispersal. In the scenario 3), the dispersal realized for each individual was stochastically drawn from the distribution of the dispersal kernel M (i, j). Therefore, the number of individuals from j staying in their patch or dispersing to the adjacent ones is drawn from a multinomial distribution with $N_{j,t}$ trials and probabilities $d_{j,t}$ of dispersing and $1 - k\,d_{j,t}$ of not dispersing. In the other simulations, the proportion of dispersing and non-dispersing individuals was fixed according to the expected values given by M (i, j). Each scenario was simulated 1000 times with $r = 2.43$, $K = 300$, $\sigma^2_d = 0.1$ and $\sigma^2_e = 0$. This specific set of parameters was chosen to match those of the experiment.

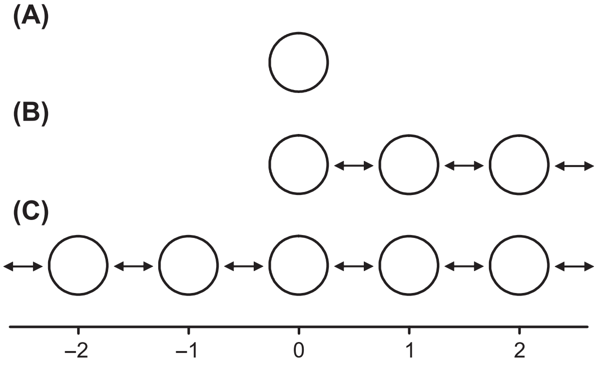

Figure 1. Schematic representation of the invaded landscape, with habitat patches (circles, the one in position 0 being the introduction site) and dispersal fluxes (arrows). (A) no dispersal from the introduction site; (B) dispersal on one side of the introduction site; (C) dispersal on both sides of the introduction site.

Because of the discrete nature of the landscape, pushed invasion fronts were expected to stop in a given patch whenever the population in it was too small to colonize the next patch. Therefore, we computed the proportion of pushed fronts i.e. invasion fronts stopping at least once during the 10 generations, for each scenario.

Experiment

Experimental design

To test experimentally the predictions from our simulations, we performed introductions of individuals in artificial landscapes and monitored their invasion over ten non-overlapping generations. Those landscapes were one-dimensional chains of patches linked to each of their neighbours. Each patch was a transparent tube (height: 100 mm, diameter: 50 mm) connected to neighbouring patches by transparent plastic pipes (length 400 mm, diameter: 5 mm). We used the minute wasp *Trichogramma chilonis* (*Hymenoptera: Trichogrammatidae*) as a biological model. This egg parasitoid of lepidopterans is used as a biological control agent for a wide range of pests (Smith 1996). Two genetically differentiated strains of *T. chilonis* caught in a field in Taiwan (T strain, 1987) and Reunion Island (R strain, 1998) were used for this experiment because they exhibited different establishment rates after introduction in isolated patches (Vercken et al. 2013). Therefore, we could expect contrasted establishment dynamics between the two strains in structured landscapes. At each generation, every patch in the landscape was provided with approx. 450 new eggs of the Mediterranean flour moth *Ephestia kuehniella* (*Lepidoptera: Pyralidae*) for them to parasitize, while the eggs from the previous generation were removed. The *E. kuehniella* eggs used during the experiment were irradiated earlier, thus preventing larvae from emerging but letting the wasps develop. Temperature and light conditions were maintained constant, with 16-h daylight (25°C) / 8-h dark (20°C) cycle and 70% humidity.

We set up a 2×2 factorial design, with two initial population sizes i.e. two or ten mated founding females and two connectivity levels at the introduction site. As in the simulations, we let individuals disperse either on only one side of the introduction site or on both sides, thus forming respectively one or two invasion fronts (Fig. 1B–C). All the designs were replicated ten times for both strains, totalling 80 monitored landscapes (Supplementary material Appendix 3). Each generation lasted nine (for T strain) or ten days (for R strain), comprised two days of adult life, during which trichogrammas could mate, lay eggs and disperse. As we considered short-distance dispersal, we focused on dispersal and colonization of patches neighbouring the already colonized ones. At each generation, one or two empty patches were added and placed on the edge of the metapopulation in the one and two-front treatments respectively. The adult phase was stopped by removing the adults to maintain non-overlapping generations during the experiment. Trichogramma larvae would then develop in *E. kuehniella* which would cause the host eggs to turn dark because of the chitinization of the parasitoid pupae. Eventually, the larvae would emerge as adults and form the next generation. Parasitized eggs were thereafter counted with the ImageJ software (Rasband 1997–2015) to estimate population sizes. Data obtained through the monitoring of parasitized egg counts were subsequently analyzed with the R software.

Invasion pattern

Invasion fronts were characterized as pushed if the colonization from small populations on the invasion front edge was hindered by mechanisms affecting their growth or their emigration. In this case, we expected a time-lag between introduction and dispersal across the landscape, during which the introduced population would build up before sending enough migrants to pursue colonization (Veit and Lewis 1996). We computed the proportion of individuals located at the introduction site for each generation: this proportion was expected to stay high during an initial time-lag before dispersal and then decrease according to a sigmoid pattern. In this case, the beginning of the dispersal phase could be detected as the sigmoid inflexion point, and evaluated as the sigmoid derivative maximum. We also expected additional stops further along the invasion process, every time the front population was too small to efficiently colonize a new patch in the next generation. We tested the relationship between population size on the font at time t and the probability that the invasion front advances in the time step $[t\ ,\ t+1]$ with a logistic regression. In order to reveal pushed invasion patterns in our experimental data, we looked for stops in the progress of the invasion front once the initial populations had started to colonize the landscape.

Invasion speed

Two different measures of invasion speed were used: the progression of the invasion fronts and the expansion of the metapopulations themselves. Front progression was measured as the number of patches between the introduction site and the furthermost colonized patch. Each front was considered separately in the two-front treatment. Metapopulation expansion was measured as the number of patches colonized in each landscape. To account for the dynamic nature of the data in time, the influence of the different explanatory factors was tested in interaction with generation. As they were patch counts, results were analyzed with a Poisson generalized linear mixed model with the *glmer* function of the *lme4* package (Bates et al. 2013), with the replicate as a random effect. Geographic strain was added as a covariate to test its impact. The best models among all candidates were selected using lowest corrected Akaike information criterion (AIC_C) (Burnham and Anderson 2004). When several models were equivalent ($\Delta AIC_C < 2$), the model with the fewest parameters was retained (Supplementary material Appendix 1 Table A1–A2).

Metapopulation sustainability

Establishment was characterized as the number of non-extinct replicates at the end of the experiment. The effects of experimental treatments on metapopulation extinction were tested with Fisher's exact tests. However, extinction events were more likely to occur at the local level because of metapopulation extinction-recolonization dynamics. Therefore, we computed the mean local extinction rate as the proportion of extinct local populations at a given generation. We also looked for declining local populations, which were populations shrinking due to other reasons rather than negative density-dependence driven by competition. We defined a local declination index as the proportion of local populations declining to lower than 50% of the carrying capacity at a given generation. The carrying capacities for strains R and T in similar environmental conditions were estimated by Vercken et al. (2013). Since the local mean extinction rate and the local declination index were both proportions we used Binomial generalized linear mixed models with the 'glmer' function of the *lme4* package (Bates et al. 2013), with the replicate as a random effect. The strain and the number of colonized patches were added as covariates. In both cases, the best models among all candidates were selected using lowest AIC_C. When several models were equivalent ($\Delta AIC_C < 2$), the model with the fewest parameters was retained (Supplementary material Appendix 1 Table A3–A6).

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.jv7n7 > (Morel-Journel et al. 2015).

Results

Model

Establishment rate

Simulations indicated that demographic stochasticity alone decreased establishment rate for the smallest initial populations, especially in presence of connectivity (Fig. 2A–B). The simulations with both demographic and environmental stochasticities ($\sigma^2_e = 2$) showed a positive impact of the introduction site connectivity on establishment for larger initial populations (Fig. 2B). In simulations with demographic stochasticity and a strong Allee effect ($A = 5$), establishment decreased sharply under the Allee threshold and decreased further with connectivity. As the introduction site was more connected, more individuals were required to reach the same establishment rate (Fig. 2C).

Invasion pattern

The simulations without Allee effect or density-dependent dispersal and deterministic dispersal exhibited different patterns depending on whether dispersal was stochastic or deterministic. Only 5.9% of the fronts simulated with deterministic dispersal were pushed (Fig. 3A), while 92.6% of those simulated with stochastic dispersal were (Fig. 3B). Any simulation including an Allee effect ($A = 5$) or positive density-dependent dispersal ($g = 0.4$) exhibited a pushed invasion pattern (Fig. 3C–D). Conversely, none of the simulated invasion fronts with negative density-dependent dispersal ($g = -0.1$) were pushed. In the scenarios with Allee effects, positive density-dependent dispersal or stochastic dispersal, the invasion front stopped until the population on the front was sufficiently large for expansion to start again (Fig. 3).

Experiment

Invasion pattern

Every experimental invasion front stopped at least once in ten generations, showing that the invasion patterns observed in the experiment were similar to the pushed invasions generated by the model. Invasion fronts stopped more often when the population on the front edge was small ($z = -3.472$, $p < 0.001$; Fig. 4A). Furthermore, the proportion of individuals located in the introduction site displayed a sigmoid pattern indicating a time-lag before the dispersal of individuals to other patches (Fig. 4B). We could therefore separate an initial population growth phase before the expected expansion phase across the landscape (Fig. 4C). A linear regression on the time of the switch between the two phases indicated that the growth phase was longer for the T strain ($t = 3.634$, $p < 0.001$) and for metapopulations in the one-front treatment ($t = 2.462$; $p = 0.016$).

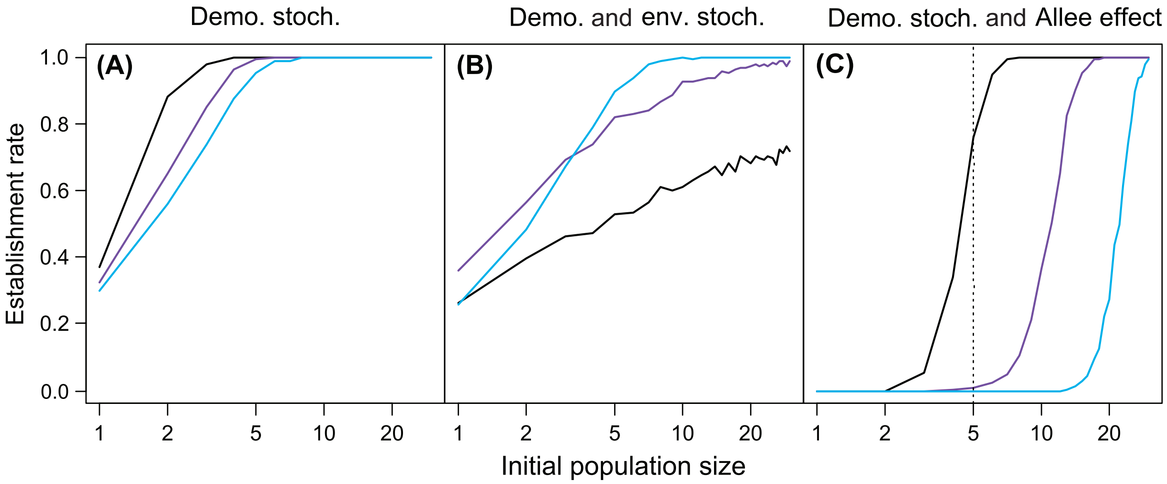

Figure 2. Mean establishment rates ten generations after introduction over 1000 simulations as a function of initial population size (in logarithmic scale), for different connectivity levels: without dispersal (black), dispersal on one side of the introduction site (purple) or dispersal on both sides of the introduction site (light blue). (A) (Demo. stoch): with demographic stochasticity alone ($\sigma^2_d = 0.1$); (B) (Demo. and env stoch): with demographic and environmental stochasticity ($\sigma^2_d = 0.1$ and $\sigma^2_e = 2$); (C) (Demo. and Allee effect): with demographic stochasticity and Allee effect ($\sigma^2_d = 0.1$ and $A = 5$), with the Allee threshold at 5 individuals (vertical dotted line).

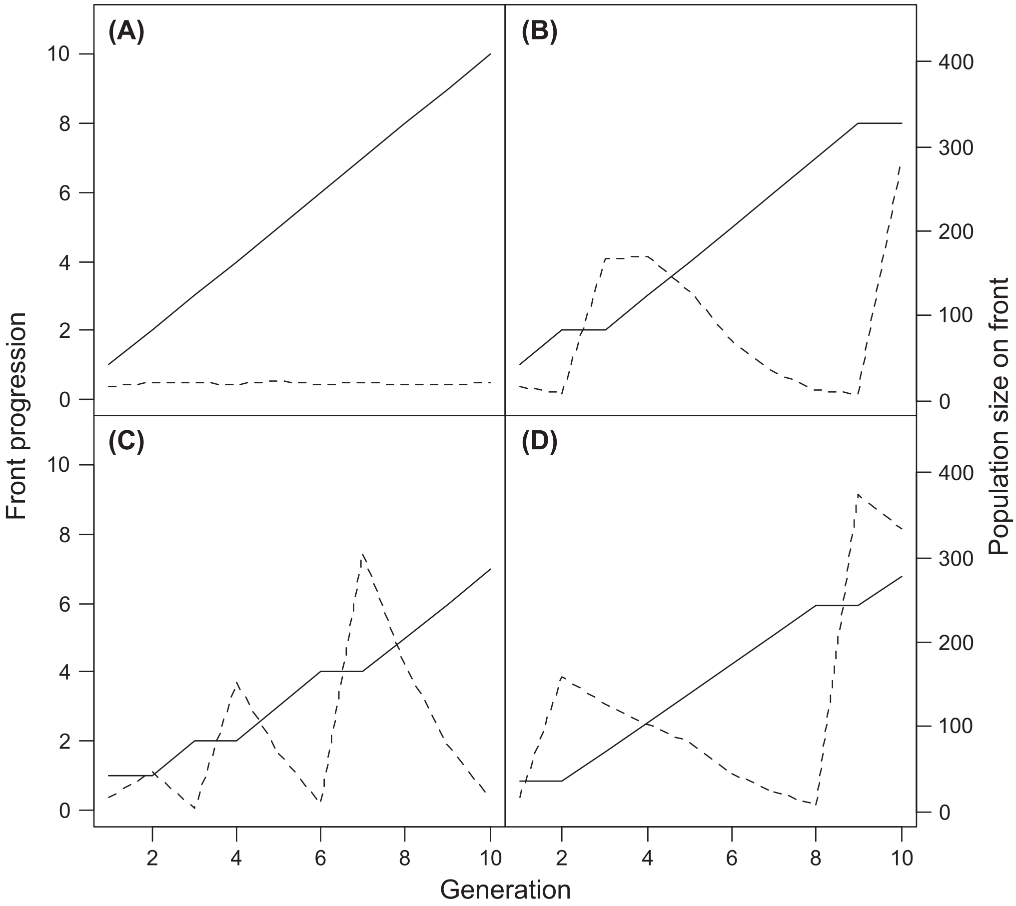

Figure 3. Example of simulated front progression (solid lines) and size of the furthermost population on the front (dashed lines) during ten generations after introduction (initial population size: 20 individuals) (A) without Allee effect or density-dependent dispersal and with deterministic dispersal; (B) without Allee effect or density-dependent dispersal and with stochastic dispersal; (C) with Allee effect ($A = 5$) and deterministic dispersal; (D) with positive density-dependent dispersal ($g = 0.4$) and deterministic dispersal.

Invasion speed

At the end of the experiment, the invasion fronts in the non-extinct replicates had advanced on average 2.48 patches (SD: 1.23). The mean speed of the invasion fronts observed during the experiment was 0.28 patches per generation, and all front speeds were greatly inferior to the one colonized patch per generation limit permitted by the experimental setting. The best model according to AIC_C explaining the front speed did not include connectivity or initial population size, indicating that the speed of each front did not depend on the number of fronts in the metapopulation. Consequently, metapopulations progressing on two fronts at the same time expanded

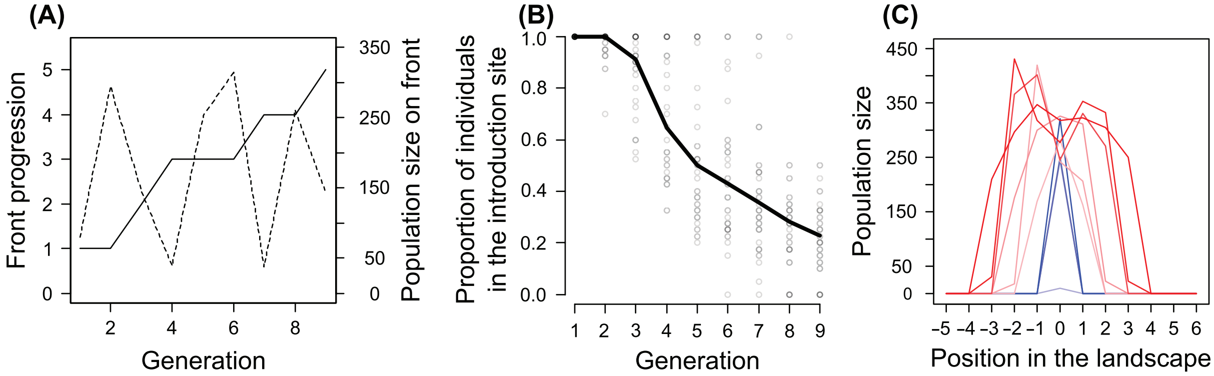

Figure 4. (A) Example of experimentally observed front progression (solid line) and size of the furthermost population on this front (dashed line) during the nine generations after introduction. (B) Population size at the introduction site relative to the number of individuals in the whole metapopulation as a function of the generation for each replicate (points) and the median value for at each generation (solid line). (C) Population sizes in an experimental metapopulation as a function of the patch position in the landscape (0 being the introduction site). Every generation is represented with solid lines during growth phase (from light to dark blue) and the expansion phase (from light to dark red).

Table 1. Explanatory variables and p-values in the models selected by using lowest corrected Akaike information criterion.

Response variable	Explanatory variable	z-value	p-value
Front progression	generation	20.802	< 0.001
	generation : strain	–2.332	0.020
Metapopulation size	generation	12.230	< 0.001
	generation : connectivity	6.661	< 0.001
	generation : strain	–3.487	< 0.001
Mean local extinction rate (growth)	colonized patches	3.936	< 0.001
	connectivity	1.898	0.058
	introduced population size	2.299	0.022
Mean local extinction rate (expansion)	strain	3.558	< 0.001
Mean local declination rate (growth)	colonized patches	2.718	0.007
Mean local declination rate (expansion)	introduced population size	–2.192	0.028
	strain	4.200	< 0.001

faster (Table 1). Both the front speed and metapopulation expansion were also slower for the T strain (Table 1).

Metapopulation sustainability

Only eight of the 80 metapopulations were completely extinct at the end of the experiment, which corresponded to an overall 90% establishment success. Fisher's exact tests indicated that there was no effect solely due to connectivity ($p = 0.71$) and only a marginal effect of initial population size on establishment success ($p = 0.057$). However, metapopulations initiated with few individuals in a more connected site exhibited significantly more establishment failures than the other factor combinations ($p = 0.021$). Results for the mean local extinction rate and the declination rates were significantly different between the two phases. During the first generations of the growth phase, both the local extinction index and the local declination index were higher in replicates where patches had been colonized (Table 1). During the expansion phase, the number of colonized patches no longer had an effect, while initial population size was negatively correlated with the declination index. During this phase, the T strain also exhibited more local extinctions and more declining populations (Table 1).

Discussion

Establishment success

Simulations exhibited a decrease in establishment success for small initial population sizes, either because of an Allee effect or because of demographic stochasticity. Moreover, this effect increased with the connectivity of the introduction site in the absence of environmental stochasticity. The experimental results confirmed the simulations by highlighting the interplay between initial population size and connectivity of the introduction site on establishment. A critical hypothesis of the model is that individuals disperse randomly, according to a diffusion process. In the experiment, the absence of correlation between front speed and the number of connections also suggests that individuals dispersed more when connectivity was higher, thus supporting this hypothesis. This result experimentally confirm the modelling results of Kanarek et al. (2013) and Drury et al. (2007), where individuals also dispersed randomly. Moreover, early secondary colonizations were associated with higher local declination index and mean extinction rates. Thus, dispersal during the growth phase corresponded to a loss of individuals and did not promote the formation of viable metapopulations. We could however expect different results if dispersal was not random.

The 90 percent establishment success in the experiment was significantly higher than those observed in natura (Williamson and Fitter 1996, Freckleton 2000, Noël et al. 2011), thus indicating that establishment was highly predictable in our laboratory microcosms. In laboratory conditions, populations do tend to experience high growth rates, thus quickly exceeding the range of sizes vulnerable to demographic stochasticity or Allee effects Nevertheless, Vercken et al. (2013) observed a significantly lower establishment success close to 40% establishment in identical experimental conditions but on isolated populations. This latter result highlights the importance of the spatial structure of the introduction area. Indeed, as individuals were introduced in several patches in structured landscapes, they were able to disperse and colonize other patches than the introduction site, thus escaping local competition. As seen in the simulations, connectivity of the introduction site to other patches also decreased the extinction risk linked to environmental stochasticity. This is because metapopulation dynamics, such as recolonization and rescue effects, can increase local populations' persistence (Brown and Kodric-Brown 1977, Hanski and Gaggiotti 2004).

Pushed colonization pattern

Both the initial growth phase and the subsequent invasion front stops suggest that secondary colonizations depend on the local dynamics of the already established populations, which would be consistent with a pushed invasion pattern (Stokes 1976). By simulation, we identified three non-exclusive mechanisms affecting the invasion pattern in such a way: Allee effects, positive density-dependent dispersal i.e. increased emigration rate with population size, and dispersal stochasticity. While previous studies have addressed the impact of the first two mechanisms on spread (Lewis and Kareiva 1993, Veit and Lewis 1996, Roques et al. 2012, Altwegg et al. 2013, Kanarek et al. 2013), this is, to our knowledge, the first study investigating the effect of the latter in a biological system. The effect of dispersal stochasticity on the invasion pattern is linked to the discrete number of individuals and the discretization of space in habitat patches (Panja 2004, Pachepsky and Levine 2011). Because the number of dispersing individuals results from the stochastic realization of each individual dispersal, the population dispersal rate variance increased when population size decreased. Therefore at low dispersal rates, there was a significant probability that small populations did not disperse at all. This decrease in invasion speed directly linked to the population dynamics behind the invasion front corresponds to the "weakly pushed" invasion fronts described by Panja (2004) (Supplementary material Appendix 4). An analogous phenomenon in continuous space is described as "pulsed invasions" by Johnson et al. (2006). In this case, long distance dispersing individuals from the core populations initiate isolated colonies way ahead of the front, which expand and eventually merge with the source population. As for pushed invasion patterns in discrete space, pulsed invasion advances occur only when those populations are large enough.

While the three underlying mechanisms all generate similar patterns, their impacts on establishment are different. Dispersal stochasticity and positive density-dependent dispersal hamper emigration, thus decreasing in the initial risk of population extinction, whereas Allee effects eliminate dispersing individuals, while emigration still occurs and thus does not mitigate extinction risk. Additional experiments were performed and analyzed by approximate Bayesian computation to investigate the presence of Allee effects or positive density-dependent dispersal in experimental *Trichogramma* populations (Supplementary material Appendix 2). We found substantial support for positive density-dependent dispersal in our experimental populations, even though migration rates remain very low (between 0.001 and 0.2). Therefore, when populations on the front were small, the observed pushed invasion pattern was mainly driven by low dispersal rates combined with dispersal stochasticity, and reinforced by positive density-dependent dispersal.

Design limits and implications for introductions in natura

Population dynamics in the context of biological invasions benefit from an abundant theoretical support as compared to the low number of experimental studies (reviewed by Hastings et al. 2005). Indeed, the latter are commonly hampered by technical and ethical limitations. Experimental microcosms are tools that may help solve these issues since they can be used to perform introductions in controlled and confined environments over numerous replicates (Drake and Kramer 2012). Yet, using such set-ups implies a tradeoff between discriminating power and realism. Thus, the approximation of landscapes as one-dimensional chains of patches connected by dispersal fluxes in our study has some limitations. On the one hand, one-dimensional landscapes are powerful tools to analyze population trajectories despite their high stochasticity (Melbourne and Hastings 2009, Giometto et al. 2014). On the other hand, considering higher dimensional landscapes would have allowed the inclusion of more complex landscape features such as patch area (Vercken et al. 2011).

In this study, we considered connectivity as the way landscape affected movement between habitat patches. By either allowing or preventing the dispersal of individuals from the introduction site, we considered an extreme case where landscape features would correspond to insurmountable barriers in natura. These barriers can be anthropogenic (Rodriguez-Freire and Crecente-Maseda 2008), but they can also be natural landscape features (Rueness et al. 2003) or variations in environmental conditions (Winemiller et al. 2008). In the context of introduced populations, such as the use of biological control agents in agriculture, landscape elements like windbreaks, hedgerows or ditches, can act as barriers to dispersal (Lovei et al. 1998, Wratten et al. 2003). By hampering emigration, those barriers do modify individual dispersal.

In a context of biocontrol, the results of this study concerning the impact of connectivity suggest that introductions in well connected landscapes correspond to an "all or nothing" strategy, where the population would either become extinct quickly or form a stable metapopulation expanding across all the landscape. Therefore, they support the "Goldilocks" hypothesis proposed by Heimpel and Asplen (2011), which suggest that medium dispersal levels are optimal for the release of biological control agents. However, we did not find in our study any evidence of an interaction between strain characteristics and landscape structure on establishment success. Indeed, one strain performed consistently better than the other, but there was no difference in the establishment pattern.

Conclusion

This study brings the first empirical confirmation that connectivity can decrease initial persistence by increasing early emigration from the introduced population, but also promote persistence in the long run by favouring the formation of a metapopulation. These empirical observations in microcosm, backed by simulation results, are a first important step for investigating the impact of connectivity on the dynamics of introduced populations and their establishment. We argue that this study could be at the basis of further investigations of this relationship, for example by considering more complex, two dimensional landscapes, or by including heterogeneity between habitat patches or the introduced species used, and eventually bridge the gap to empirical studies concerning the colonization of natural landscapes.

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References

Altwegg, R. et al. 2013. Density-dependent dispersal and the speed of range expansions. – Divers. Distrib. 19: 60–68.

Bates, D. et al. 2013. lme4: linear mixed-effects models using Eigen and S4. – <https://cran.r-project.org/package=lme4>

Bonnefon, O. et al. 2014. The spatio-temporal dynamics of neutral genetic diversity. – Ecol. Complex. 20: 282–292.

Brassil, C. E. 2001. Mean time to extinction of a metapopulation with an Allee effect. – Ecol. Modell. 143: 9–16.

Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography – effect of immigration on extinction. – Ecology 58: 445–449.

Burnham, K. P. and Anderson, D. R. 2004. Multimodel inference – understanding AIC and BIC in model selection. – Sociol. Meth. Res. 33: 261–304.

Calabrese, J. M. and Fagan, W. F. 2004. A comparison-shopper's guide to connectivity metrics. – Front. Ecol. Environ. 2: 529–536.

Courchamp, F. et al. 2008. Allee effects in ecology and conservation. – Oxford Univ. Press.

Drake, J. M. and Kramer, A. M. 2012. Mechanistic analogy: how microcosms explain nature. – Theor. Ecol. 5: 433–444.

Drury, K. L. S. et al. 2007. Immigration events dispersed in space and time: factors affecting invasion success. – Ecol. Modell. 206: 63–78.

Ebenhard, T. 1991. Colonization in metapopulations – a review of theory and observations. – Biol. J. Linn. Soc. 42: 105–121.

Fauvergue, X. et al. 2012. The biology of small, introduced populations, with special reference to biological control. – Evol. Appl. 5: 424–443.

Freckleton, R. P. 2000. Biological control as a learning process. – Trends Ecol. Evol. 15: 263–264.

Garnier, J. et al. 2012. Success rate of a biological invasion in terms of the spatial distribution of the founding population. – Bull. Math. Biol. 74: 453–473.

Giometto, A. et al. 2014. Emerging predictable features of replicated biological invasion fronts. – Proc. Natl Acad. Sci. USA 111: 297–301.

Hanski, I. and Gaggiotti, O. E. 2004. Ecology, genetics, and evolution of metapopulations. – Academic Press.

Hastings, A. et al. 2005. The spatial spread of invasions: new developments in theory and evidence. – Ecol. Lett. 8: 91–101.

Hayes, K. and Barry, S. 2008. Are there any consistent predictors of invasion success? – Biol. Invas. 10: 483–506.

Heg, D. et al. 2008. Experimentally induced helper dispersal in colonially breeding cooperative cichlids. – Environ. Biol. Fish. 83: 191–206.

Heimpel, G. E. and Asplen, M. K. 2011. A 'Goldilocks' hypothesis for dispersal of biological control agents. – Biocontrol 56: 441–450.

Johnson, D. M. et al. 2006. Allee effects and pulsed invasion by the gypsy moth. – Nature 444: 361–363.

Jonsen, I. D. and Taylor, P. D. 2000. Fine-scale movement behaviors of calopterygid damselflies are influenced by landscape structure: an experimental manipulation. – Oikos 88: 553–562.

Kanarek, A. et al. 2013. Allee effects, aggregation, and invasion success. – Theor. Ecol. 6: 153–164.

Kean, J. M. and Barlow, N. D. 2000. Effects of dispersal on local population increase. – Ecol. Lett. 3: 479–482.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911–927.

Lande, R. et al. 2003. Stochastic population dynamics in ecology and conservation. – Oxford Univ. Press.

Lewis, M. A. and Kareiva, P. 1993. Allee dynamics and the spread of invading organisms. – Theor. Popul. Biol. 43: 141–158.

Lovei, G. L. et al. 1998. Dispersal and effects of barriers on the movement of the New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. – J. Appl. Entomol. 122: 115–120.

Melbourne, B. A. and Hastings, A. 2009. Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. – Science 325: 1536–1539.

Morel-Journel, T. et al. 2015. Data from: The highs and lows of dispersal: how connectivity and initial population size jointly shape establishment dynamics in discrete landscapes. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.jv7n7>.

Noël, F. et al. 2011. Establishment success of 25 rare wetland species introduced into restored habitats is best predicted by ecological distance to source habitats. – Biol. Conserv. 144: 602–609.

Pachepsky, E. and Levine, J. M. 2011. Density dependence slows invader spread in fragmented landscapes. – Am. Nat. 177: 18–28.

Panja, D. 2004. Effects of fluctuations on propagating fronts. – Phys. Rep.-Rev. Sec. Phys. Lett. 393: 87–174.

Parlato, E. H. and Armstrong, D. P. 2013. Predicting post-release establishment using data from multiple reintroductions. – Biol. Conserv. 160: 97–104.

Pratt, S. C. et al. 2002. Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. – Behav. Ecol. Sociobiol. 52: 117–127.

Rasband, W. S. 1997–2015. ImageJ. – Natl Inst.s of Health.

Rodriguez-Freire, M. and Crecente-Maseda, R. 2008. Directional connectivity of wolf (*Canis lupus*) populations in northwest spain and anthropogenic effects on dispersal patterns. – Environ. Model. Assess. 13: 35–51.

Roques, L. et al. 2012. Allee effect promotes diversity in traveling waves of colonization. – Proc. Natl Acad. Sci. USA 109: 8828–8833.

Rueness, E. K. et al. 2003. Ecological and genetic spatial structuring in the Canadian lynx. – Nature 425: 69–72.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. – Annu. Rev. Ecol. Evol. Syst. 40: 81–102.

Smith, S. M. 1996. Biological control with *Trichogramma*: advances, successes, and potential of their use. – Annu. Rev. Entomol. 41: 375–406.

Stokes, A. N. 1976. On two types of moving front in quasilinear diffusion. – Math. Biosci. 31: 307–315.

Taylor, P. D. et al. 1993. Connectivity is a vital element of landscape structure. – Oikos 68: 571–573.

Veit, R. R. and Lewis, M. A. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. – Am. Nat. 148: 255–274.

Vercken, E. et al. 2011. Critical patch size generated by Allee effect in gypsy moth, *Lymantria dispar* (L.). – Ecol. Lett. 14: 179–186.

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.

Wang, M. H. and Kot, M. 2001. Speeds of invasion in a model with strong or weak Allee effects. – Math. Biosci. 171: 83–97.

Williamson, M. and Fitter, A. 1996. The varying success of invaders. – Ecology 77: 1661–1666.

Winemiller, K. O. et al. 2008. Fish assemblages of the Casiquiare River, a corridor and zoogeographical filter for dispersal between the Orinoco and Amazon basins. – J. Biogeogr. 35: 1551–1563.

Wratten, S. D. et al. 2003. Field boundaries as barriers to movement of hover flies (Diptera : Syrphidae) in cultivated land. – Oecologia 134: 605–611.

Supplementary material (available online as Appendix oik.02718 at <www.oikosjournal.org/readers/appendix>). Appendix 1–4.