BIOLOGY
LETTERS

rsbl.royalsocietypublishing.org

Research

Cite this article: Morel-Journel T, Piponiot C, Vercken E, Mailleret L. 2016 Evidence for an optimal level of connectivity for establishment and colonization. *Biol. Lett.* **12**: 20160704.
http://dx.doi.org/10.1098/rsbl.2016.0704

Received: 30 August 2016
Accepted: 7 November 2016

Subject Areas:
ecology

Keywords:
connectivity, establishment, individual-based model, introduction, microcosm

Author for correspondence:
Thibaut Morel-Journel
e-mail: thibaut.moreljournel@laposte.net

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3577181.

THE ROYAL SOCIETY
PUBLISHING

Population ecology

Evidence for an optimal level of connectivity for establishment and colonization

Thibaut Morel-Journel[1], Camille Piponiot[1], Elodie Vercken[1] and Ludovic Mailleret[1,2]

[1]Université Côte d'Azur, INRA, CNRS, ISA, 06900 Sophia Antipolis, France
[2]Université Côte d'Azur, Inria, INRA, CNRS, UPMC Univ. Paris 06, 06900 Sophia Antipolis, France

TM-J, 0000-0002-9124-2894

Dispersal is usually associated with the spread of invasive species, but it also has two opposing effects, one decreasing and the other increasing the probability of establishment. Indeed, dispersal both slows population growth at the site of introduction and increases the likelihood of surrounding habitat being colonized. The connectivity of the introduction site is likely to affect dispersal, and, thus, establishment, according to the dispersal behaviour of individuals. Using individual-based models and microcosm experiments on minute wasps, we demonstrated the existence of a hump-shaped relationship between connectivity and establishment in situations in which individual dispersal resembled a diffusion process. These results suggest that there is an optimal level of connectivity for the establishment of introduced populations locally at the site of introduction, and regionally over the whole landscape.

1. Introduction

Understanding the mechanisms underlying the establishment and spread of introduced species is critical to prevent biological invasions and maximizes the success of planned introductions, such as the release of biocontrol agents. Dispersal is often associated with the spread of the introduced individuals across their new environment [1,2], but it can also play a key role earlier in the invasion process. Indeed, early emigration slows the growth of the already small introduced population [3], and this can lead to establishment failure [4,5]. However, the emigrating individuals can also colonize other habitats, thereby potentially increasing the persistence of the introduction site [6], or facilitating its recolonization after an extinction event [7]. As individuals are susceptible to disperse as soon as they are introduced, a knowledge of the interaction between these two phenomena in the few first generations after introduction is crucial for the accurate estimation of establishment probabilities [8,9]. To initiate dispersal, some species rely on biological signals, such as physiological condition [10,11] or quorum sensing [12]. For other species with movement patterns more closely resembling diffusion processes, landscape features have a much greater effect on dispersal propensity (e.g. [13–15]). We investigated the impact of introduction site connectivity—i.e. the number of connections to other patches [9,16]—on establishment success for these two types of dispersal.

We developed an individual-based model describing population dynamics in discrete space, and simulated invasions at introduction sites with various levels of connectivity. We also evaluated the impact of two mechanisms hampering colonization success: dispersal mortality and Allee effects [17,18]. Dispersal mortality eliminates dispersing individuals, and Allee effects reduce the persistence of the newly formed colonies during spread. We then tested the predictions of the model through the artificial introduction of minute parasitoid wasps (Trichogramma chilonis) into artificial laboratory landscapes. We found a hump-shaped relationship between connectivity and establishment for species displaying diffusion-like dispersal. This suggests that there is an optimal level of connectivity for maximal success in the establishment of introduced populations at the local and landscape scales.

2. Material and methods

(a) Model

We simulated invasions in landscapes consisting of one introduction site, connected to k peripheral patches. Each peripheral patch had two connections: one to the introduction site and one outside the landscape. Individuals in peripheral patches could therefore exit the landscape, with no possibility of return. The individual-based model used is described in electronic supplementary material, 1. We considered two extreme patterns of dispersal behaviour: random and predetermined movements. The individuals with random dispersal behaviour were considered to move randomly within patches, in a diffusion-like manner [19]. Their probability of emigrating, p, increased with the number of connections, n, as:

$$p = 1 - (1 - p_1)^n, \qquad (2.1)$$

with p_1 the probability that an individual emigrated when $n = 1$. Individuals with a predetermined dispersal behaviour emigrated with a constant probability, regardless of n. Individuals surviving dispersal (with a probability $1 - m$) were distributed evenly between the neighbouring patches. The reproduction of individuals was affected by a parameter γ describing the intensity of Allee effects. Other parameters controlled the probability of being able to reproduce (r), intraspecific competition (α), fecundity (β) and juvenile survival (s).

Model simulations were performed with R [20], for $r = 0.4$, $s = 0.1$, $\alpha = 0.01$, $\beta = 30$, $p_1 = 0.1$ for random dispersal behaviour, and with $p = 0.19$ for predetermined dispersal behaviour. For these values, the probability of emigration from peripheral patches ($n = 2$) was the same for both types of dispersal behaviour. We tested values of k between 1 and 30, combined with Allee effects, dispersal mortality or neither of these mechanisms. Each parameter combination was simulated 5000 times, because of the stochastic nature of the model. After three generations, we calculated the proportion of simulations for which there were individuals (i) at the introduction site, (ii) in at least one of the peripheral patches, (iii) in both the introduction site and peripheral patches. We calculated the proportion of the deviance explained by logistic regressions including the number of peripheral patches k, the strength of the Allee effect and the strength of dispersal mortality as explanatory factors.

(b) Experiment

We introduced Trichogramma chilonis into laboratory microcosms and monitored population dynamics for three generations. The experimental set-up is described in electronic supplementary material, 1. The landscapes used were similar to those in the simulations, with 1, 7 or 15 peripheral patches. The experiment was replicated 15 times for each treatment, and each treatment was split into three balanced blocks. We determined two variables: the extinction rate at the introduction site and the rate of colonization of the peripheral patches. The extinction rate was calculated as the proportion of replicates for which extinction occurred at least once at the introduction site over the course of the experiment. The rate of colonization was calculated as the proportion of replicates for which at least one colonization event occurred outside the introduction site. These variables were analysed with binomial generalized linear mixed models, with experimental block as a random effect. We checked for potential nonlinear relationships by testing a linear and a quadratic relationship to the number of connections, and selected the best model according to lowest AIC_C [21].

Table 1. Proportion of the deviance in the simulated data explained by the variables. The impact of connectivity (parameter *n* between 1 and 30), dispersal mortality (parameter $m = 0$ or $m = 0.7$) and Allee effect (parameter $\gamma = 0$ or $\gamma = 0.3$) was tested using logistic regressions. The percentages correspond to the proportion of deviance explained by the model including each variable, compared with a null model without the variable.

dispersal behaviour	variable	extinction (% deviance)	colonization (% deviance)
random	connectivity	25.9	26.7
	dispersal mortality	< 0.01	17.1
	Allee effect	2.9	12.8
predetermined	connectivity	< 0.01	< 0.01
	dispersal mortality	< 0.01	9.1
	Allee effect	0.4	8.4

3. Results

Simulations confirmed that introduction site connectivity had no impact on colonization or extinction when the dispersal behaviour of individuals was predetermined (table 1 and figure 1a–c). However, when dispersal behaviour was random, connectivity increased the extinction risks at the introduction site, and the occupancy of peripheral patches (table 1 and figure 1d). The proportion of simulations for which the introduction site and the peripheral patches were colonized was therefore hump-shaped, with an optimum for intermediate connectivity levels (figure 1d–f). Sensitivity analyses (electronic supplementary material, 2) indicated that the existence of an optimum was mostly robust to variation in population growth parameters. Similarly, changes in the value of the dispersal parameter p_1 only shifted the optimal connectivity value. Overall, the inclusion of dispersal mortality or Allee effects consistently decreased the rate of peripheral patch colonization (figure 1b,c,e,f). However, it had no qualitative effect on the relationship between connectivity and persistence or colonization, with the exception of a negative impact of Allee effects on the colonization rate for $k > 5$ and predetermined dispersal behaviour (figure 1f).

The extinction rate at the introduction site increased with the number of peripheral patches to which this site was connected (Wald test, $z = -2.087$, $p = 0.037$). Colonization of peripheral patches was well explained by a model accounting for both linear (Wald test, $z = 2.759$, $p = 0.0058$) and quadratic (Wald test, $z = -2.825$, $p = 0.0047$) effects of connectivity, with an optimum for seven connections. Therefore, the proportion of replicates in which the introduction site persisted and peripheral patches were colonized was also maximal for intermediate values (figure 2).

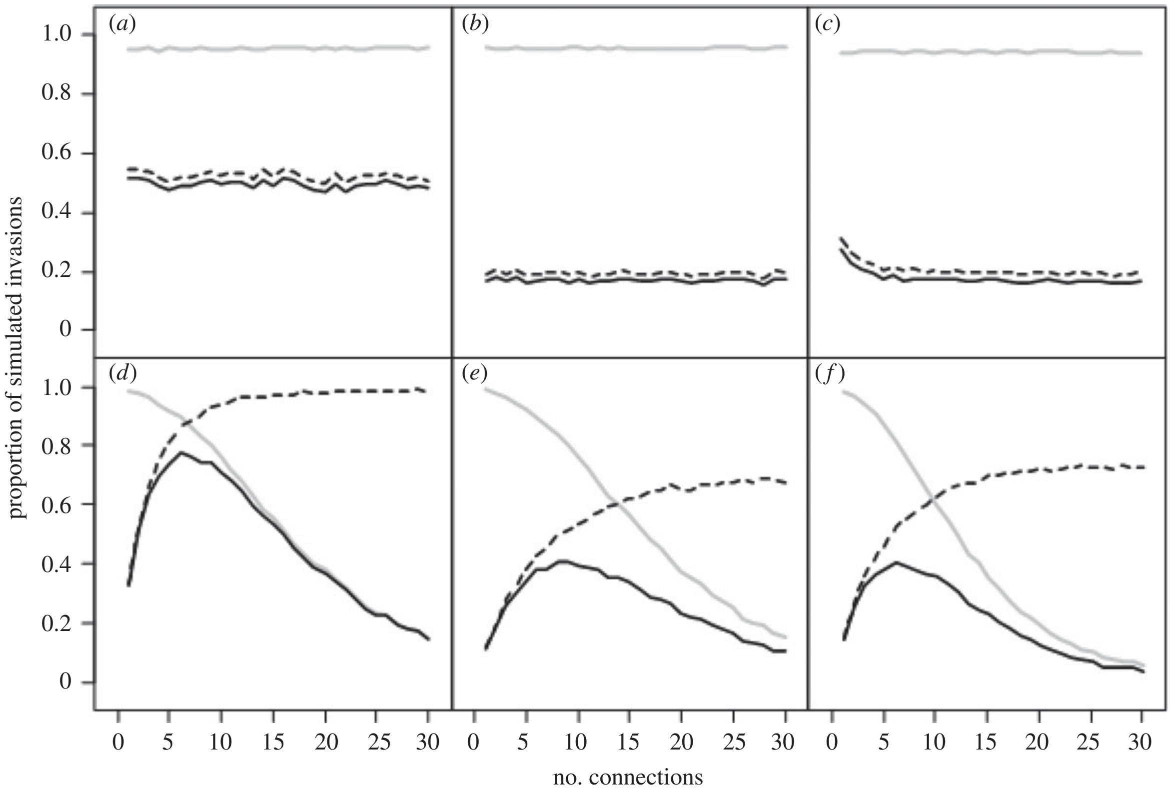

Figure 1. Proportion of the 5000 simulations for which there was no extinction event at the introduction site (grey lines), peripheral patches were colonized (dashed lines) or both (solid lines), for predetermined dispersal and (*a*) $m = 0$ and $\gamma = 0$; (*b*) $m = 0.7$ and $\gamma = 0$; (*c*) $m = 0$ and $\gamma = 0.3$; for random dispersal and (*d*) $m = 0$ and $\gamma = 0$; (*e*) $m = 0.7$ and $\gamma = 0$; (*f*) $m = 0$ and $\gamma = 0.3$.

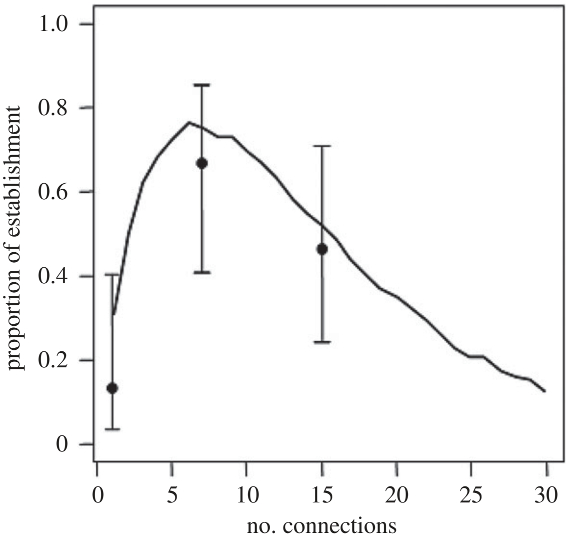

Figure 2. Proportion of experimental replicates for which there was no extinction event at the introduction site and peripheral patches were colonized (dots), with estimated 95% CIs, and the proportion of the 5000 simulations for which there was no extinction event at the introduction site and peripheral patches were colonized, from figure 1*d* (line).

4. Discussion

We considered two threats faced by introduced populations early in the invasion process: a failure to form a persistent population at the introduction site, and a failure to colonize other habitats. Simulations and experiments confirmed the impact of introduction site connectivity on these two risks, when connectivity had an impact on the likelihood of individual dispersal. At high levels of connectivity, emigration from the introduction site was higher during the first few generations, resulting in a risk of extinction of the introduced population. Previous studies found a negative impact of dispersal on establishment, linked to Allee effects [4,5,22]. In our simulations, we observed a similar effect when only demographic stochasticity was taken into account. At low levels of connectivity, the introduced populations did not send out enough dispersing individuals to colonize other patches, resulting in a lower probability of establishment. The positive effects of multiple colonies are well known in the framework of metapopulations [7]. Most metapopulations are studied at near-equilibrium, but the notion of a minimal number of local populations to ensure long-term persistence has been considered through the concepts of minimum viable metapopulation size [23] or metapopulation invasion capacity [24].

This study highlights the major role played by landscape features in the establishment of introduced populations. We demonstrated, both experimentally and by simulation, the existence of optimal connectivity levels for invasion, at which the introduced population can persist locally and colonize other patches in the landscape. Given the generality of our conclusions, similar results are expected among species with diffusion-like dispersal. Our results provide further support to the ‘Goldilocks effect’ theorized by Heimpel & Asplen [25]. They proposed that biocontrol agents with intermediate dispersal capabilities will be the most efficient. As dispersal is determined by organisms’ abilities and environmental characteristics, we also advocate for choosing introduction sites with intermediate levels of connectivity to maximize establishment.

Data accessibility. The data and code used to perform this study are available on the Dryad Digital Repository, under the provisional doi:10.5061/dryad.p0mf1.

Authors' contributions. T.M.-J., E.V. and L.M. designed the models and experiments; T.M.-J. and C.P. carried out the simulations, experiments and data analyses; all authors participated in the writing of the manuscript and gave their final approval for publication, and agree to be accountable for the content therein.

Competing interests. The authors have no competing interests to declare.

Funding. This study was funded by the Plant Health and Environment Department of the INRA and the University of Nice Sophia Antipolis. The funders had no role in study design, data collection and analysis, the decision to publish or preparation of the manuscript.

Acknowledgements. The authors would like to thank the contribution of the anonymous handling editor and the reviewers who helped improve this article.

References

1. With KA. 2002 The landscape ecology of invasive spread. *Conserv. Biol*. **16**, 1192–1203. (doi:10.1046/j.1523-1739.2002.01064.x)
2. Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM. 2011 A proposed unified framework for biological invasions. *Trends Ecol. Evol*. **26**, 333–339. (doi:10.1016/j.tree.2011.03.023)
3. Kean JM, Barlow ND. 2000 Effects of dispersal on local population increase. *Ecol. Lett*. **3**, 479–482. (doi:10.1111/j.1461-0248.2000.00183.x)
4. Robinet C, Lance DR, Thorpe KW, Onufrieva KS, Tobin PC, Liebhold AM. 2008 Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *J. Anim. Ecol*. **77**, 966–973. (doi:10.1111/j.1365-2656.2008.01417.x)
5. Kanarek AR, Webb CT, Barfield M, Holt RD. 2013 Allee effects, aggregation, and invasion success. *Theor. Ecol*. **6**, 153–164. (doi:10.1007/s12080-012-0167-z)
6. Brown JH, Kodric-Brown A. 1977 Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445. (doi:10.2307/1935620)
7. Hanski I, Gaggiotti O. 2004 *Ecology, genetics and evolution of metapopulations*. San Diego, CA: Academic Press.
8. Taylor PD, Fahrig L, Henein K, Merriam G. 1993 Connectivity is a vital element of landscape structure. *Oikos* **68**, 571. (doi:10.2307/3544927)
9. Tischendorf L, Fahrig L. 2000 On the usage and measurement of landscape connectivity. *Oikos* **90**, 7–19. (doi:10.1034/j.1600-0706.2000.900102.x)
10. Nunes S, Duniec TR, Schweppe SA, Holekamp KE. 1999 Energetic and endocrine mediation of natal dispersal behavior in Belding's ground squirrels. *Horm. Behav*. **35**, 113–124. (doi:10.1006/hbeh.1998.1504)
11. Edeline E, Lambert P, Rigaud C, Elie P. 2006 Effects of body condition and water temperature on *Anguilla anguilla* glass eel migratory behavior. *J. Exp. Mar. Biol. Ecol*. **331**, 217–225. (doi:10.1016/j.jembe.2005.10.011)
12. Pratt S, Mallon E, Sumpter D, Franks N. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol*. **52**, 117–127. (doi:10.1007/s00265-002-0487-x)
13. Gustafson EJ, Gardner RH. 1996 The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**, 94–107. (doi:10.2307/2265659)
14. Haddad NM, Bowne DR, Cunningham A, Danielson BJ, Levey DJ, Sargent S, Spira T. 2003 Corridor use by diverse taxa. *Ecology* **84**, 609–615. (doi:10.1890/0012-9658(2003)084[0609:CUBDT]2.0.CO;2)
15. Schtickzelle N, Mennechez G, Baguette M, Mennechez G. 2006 Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* **87**, 1057–1065. (doi:10.1890/0012-9658(2006)87[1057:DDWHFI]2.0.CO;2)
16. Moilanen A, Hanski I. 2001 On the use of connectivity measures in spatial ecology. *Oikos* **95**, 147–151. (doi:10.1034/j.1600-0706.2001.950116.x)
17. Allee WC. 1949 *Principles of animal ecology*. Philadelphia, PA: Saunders.
18. Courchamp F, Berec L, Gascoigne J. 2008 *Allee effects in ecology and conservation*. Oxford, UK: Oxford University Press. [cited 2016 Jan. 10]
19. Okubo A, Levin SA. 2001 *Diffusion and ecological problems: modern perspectives*. New York, NY: Springer New York. [cited 2016 Jan. 10]
20. R Core Team. 2015 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
21. Burnham KP, Anderson DR. 2004 Multimodel inference understanding AIC and BIC in model selection. *Sociol. Methods Res*. **33**, 261–304. (doi:10.1177/0049124104268644)
22. Lewis MA, Kareiva P. 1993 Allee Dynamics and the spread of invading organisms. *Theor. Popul. Biol*. **43**, 141–158. (doi:10.1006/tpbi.1993.1007)
23. Hanski I, Moilanen A, Gyllenberg M. 1996 Minimum viable metapopulation size. *Am. Nat*. **147**, 527–541. (doi:10.1086/285864)
24. Ovaskainen O, Hanski I. 2001 Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theor. Popul. Biol*. **60**, 281–302. (doi:10.1006/tpbi.2001.1548)
25. Heimpel GE, Asplen MK. 2011 A 'Goldilocks' hypothesis for dispersal of biological control agents. *BioControl* **56**, 441–450. (doi:10.1007/s10526-011-9381-7)