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1 Evidence for an optimal level of connectivity for establishment and colonisation

2

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10 **ABSTRACT**

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

22

23 **KEY WORDS**

24 connectivity; establishment; individual-based model; introduction; microcosm

25 INTRODUCTION

26 Understanding the mechanisms underlying the establishment and spread of introduced
27 species is critical to prevent biological invasions and maximize the success of planned
28 introductions, such as the release of biocontrol agents. Dispersal is often associated with the
29 spread of the introduced individuals across their new environment [1,2], but it can also play a
30 key role earlier in the invasion process. Indeed, early emigration slows the growth of the
31 already small introduced population [3], and this can lead to establishment failure [4,5].
32 However, the emigrating individuals can also colonise other habitats, thereby potentially
33 increasing the persistence of the introduction site [6], or facilitating its recolonization after an
34 extinction event [7]. As individuals are susceptible to disperse as soon as they are introduced,
35 a knowledge of the interaction between these two phenomena in the few first generations after
36 introduction is crucial for the accurate estimation of establishment probabilities [8,9]. To
37 initiate dispersal, some species rely on biological signals, such as physiological condition
38 [10,11] or quorum sensing [12]. For other species with movement patterns more closely
39 resembling diffusion processes, landscape features have a much greater effect on dispersal
40 propensity [e.g. 13–15]. We investigated the impact of introduction site connectivity — i.e.
41 the number of connections to other patches [9,16] — on establishment success for these two
42 types of dispersal.

43 We developed an individual-based model describing population dynamics in discrete
44 space, and simulated invasions at introduction sites with various levels of connectivity. We
45 also evaluated the impact of two mechanisms hampering colonisation success: dispersal
46 mortality and Allee effects [17,18]. Dispersal mortality eliminates dispersing individuals, and
47 Allee effects reduce the persistence of the newly formed colonies during spread. We then
48 tested the predictions of the model through the artificial introduction of minute parasitoid
49 wasps (*Trichogramma chilonis*) into artificial laboratory landscapes. We found a hump-

50 shaped relationship between connectivity and establishment for species displaying diffusion-
51 like dispersal. This suggests that there is an optimal level of connectivity for maximal success
52 in the establishment of introduced populations at the local and landscape scales.

53

54 MATERIALS AND METHODS

55 *Model*

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

$$64 \quad p = 1 - (1 - p_1)^n, \quad (1)$$

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

71 Model simulations were performed with R [20], for $r = 0.4, s = 0.1, \alpha = 0.01, \beta =$
72 $30, p_1 = 0.1$ for random dispersal behaviour, and with $p = 0.19$ for predetermined dispersal
73 behaviour. For these values, the probability of emigration from peripheral patches ($n = 2$) was
74 the same for both types of dispersal behaviour. We tested values of k between 1 and 30,

75 combined with Allee effects, dispersal mortality or neither of these mechanisms. Each
76 parameter combination was simulated 5000 times, because of the stochastic nature of the
77 model. After three generations, we calculated the proportion of simulations for which there
78 were individuals (i) at the introduction site, (ii) in at least one of the peripheral patches, (iii) in
79 both the introduction site and peripheral patches. We calculated the proportion of the deviance
80 explained by logistic regressions including the number of peripheral patches k , the strength of
81 the Allee effect and the strength of dispersal mortality as explanatory factors.

82

83 *Experiment*

84 We introduced *Trichogramma chilonis* into laboratory microcosms and monitored
85 population dynamics for three generations. The experimental setup is described in Electronic
86 Supplementary Material 1. The landscapes used were similar to those in the simulations, with
87 one, seven or 15 peripheral patches. The experiment was replicated 15 times for each
88 treatment, and each treatment was split into three balanced blocks. We determined two
89 variables: the extinction rate at the introduction site and the rate of colonisation of the
90 peripheral patches. The extinction rate was calculated as the proportion of replicates for which
91 extinction occurred at least once at the introduction site over the course of the experiment.
92 The rate of colonisation was calculated as the proportion of replicates for which at least one
93 colonisation event occurred outside the introduction site. These variables were analysed with
94 binomial generalised linear mixed models, with experimental block as a random effect. We
95 checked for potential non-linear relationships, by testing a linear and a quadratic relationship
96 to the number of connections, and selected the best model according to lowest AIC_C[21].

97

98 **RESULTS**

99 Simulations confirmed that introduction site connectivity had no impact on

100 colonisation or extinction when the dispersal behaviour of individuals was predetermined
101 (Table 1, Figure 1A,B,C). However, when dispersal behaviour was random, connectivity
102 increased the extinction risks at the introduction site, and the occupancy of peripheral patches
103 (Table 1, Figure 1D). The proportion of simulations for which the introduction site and the
104 peripheral patches were colonised was therefore hump-shaped, with an optimum for
105 intermediate connectivity levels (Figure 1D, E, F). Sensitivity analyses (Electronic
106 Supplementary Material 2) indicated that the existence of an optimum was mostly robust to
107 variation in population growth parameters. Similarly, changes in the value of the dispersal
108 parameter p_1 only shifted the optimal connectivity value. Overall, the inclusion of dispersal
109 mortality or Allee effects consistently decreased the rate of peripheral patch colonisation
110 (Figure 1B, C, E, F). However, it had no qualitative effect on the relationship between
111 connectivity and persistence or colonisation, with the exception of a negative impact of Allee
112 effects on the colonisation rate for $k > 5$ and predetermined dispersal behaviour (Figure 1F).

113 The extinction rate at the introduction site increased with the number of peripheral
114 patches to which this site was connected (Wald test, $z = -2.087, p = 0.037$). Colonisation of
115 peripheral patches was well explained by a model accounting for both linear (Wald test,
116 $z = 2.759, p = 0.0058$) and quadratic (Wald test, $z = -2.825, p = 0.0047$) effects of
117 connectivity, with an optimum for seven connections. Therefore, the proportion of replicates
118 in which the introduction site persisted and peripheral patches were colonized was also
119 maximal for intermediate values (Figure 2).

120

121 **DISCUSSION**

122 We considered two threats faced by introduced populations early in the invasion
123 process: a failure to form a persistent population at the introduction site, and a failure to
124 colonise other habitats. Simulations and experiments confirmed the impact of introduction site

125 connectivity on these two risks, when connectivity had an impact on the likelihood of
126 individual dispersal. At high levels of connectivity, emigration from the introduction site was
127 higher during the first few generations, resulting in a risk of extinction of the introduced
128 population. Previous studies found a negative impact of dispersal on establishment, linked to
129 Allee effects [4,5,22]. In our simulations, we observed a similar effect when only
130 demographic stochasticity was taken into account. At low levels of connectivity, the
131 introduced populations did not send out enough dispersing individuals to colonise other
132 patches, resulting in a lower probability of establishment. The positive effects of multiple
133 colonies are well known in the framework of metapopulations [7]. Most metapopulations are
134 studied at near-equilibrium, but the notion of a minimal number of local populations to ensure
135 long-term persistence has been considered through the concepts of minimum viable
136 metapopulation size [23] or metapopulation invasion capacity [24].

137 This study highlights the major role played by landscape features in the establishment
138 of introduced populations. We demonstrated, both experimentally and by simulation, the
139 existence of optimal connectivity levels for invasion, at which the introduced population can
140 persist locally and colonise other patches in the landscape. Given the generality of our
141 conclusions, similar results are expected among species with diffusion-like dispersal. Our
142 results provide further support to the “Goldilocks effect” theorized by Heimpel and Asplen
143 [25]. They proposed that biocontrol agents with intermediate dispersal capabilities will be the
144 most efficient. Since dispersal is determined by organisms’ abilities and environmental
145 characteristics, we also advocate for choosing introduction sites with intermediate levels of
146 connectivity to maximize establishment.

147 **ETHICS STATEMENT**

148 The authors have no ethics to declare.

149

150 **DATA ACCESSIBILITY**

151 The data and code used to perform this study will be made available on Dryad upon
152 acceptance of the article.

153

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158

159 **CONTRIBUTIONS**

160 TMJ, EV and LM designed the models and experiments; TMJ and CP carried out the
161 simulations, experiments and data analyses; all authors participated in the writing of the
162 manuscript and gave their final approval for publication, and agree to be accountable for the
163 content therein.

164

165 **COMPETING INTERESTS**

166 The authors have no competing interests to declare.

167

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230 **TABLE LEGENDS**

231

232 **Table 1:** Proportion of the deviance in the simulated data explained by the variables

233

234 **FIGURE LEGENDS**

235

236 **Figure 1:** Proportion of the 5000 simulations for which there was no extinction event at the
237 introduction site (grey), peripheral patches were colonised (dashed line) or both (solid line),
238 for predetermined dispersal and A: $m = 0$ and $\gamma = 0$; B: $m = 0.7$ and $\gamma = 0$; C: $m = 0$ and
239 $\gamma = 0.3$; for random dispersal and D: $m = 0$ and $\gamma = 0$; E: $m = 0.7$ and $\gamma = 0$; F: $m = 0$ and
240 $\gamma = 0.3$.

241

242 **Figure 2:** Proportion of experimental replicates for which there was no extinction event at the
243 introduction site and peripheral patches were colonised (dots), with estimated 95% confidence
244 intervals, and the proportion of the 5000 simulations for which there was no extinction event
245 at the introduction site and peripheral patches were colonised, from figure 2D (line).