Local adaptation, dispersal evolution, and the spatial eco-evolutionary dynamics of invasion

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Abstract

Local adaptation and dispersal evolution are key evolutionary processes shaping the invasion dynamics of populations colonizing new environments. Yet their interaction is largely unresolved. Using a single-species population model along a one-dimensional environmental gradient, we show how local competition and dispersal jointly shape the eco-evolutionary dynamics and speed of invasion. From a focal introduction site, the generic pattern predicted by our model features a temporal transition from wave-like to pulsed invasion. Each regime is driven primarily by local adaptation, while the transition is caused by eco-evolutionary feedbacks mediated by dispersal. The interaction range and cost of dispersal arise as key factors of the duration and speed of each phase. Our results demonstrate that spatial eco-evolutionary feedbacks along environmental gradients can drive strong temporal variation in the rate and structure of population spread, and must be considered to better understand and forecast invasion rates and range dynamics.

Introduction

In the current era of human-mediated climate, landscape and ecosystem changes, the conservation and management of biodiversity makes it crucial to understand what governs the growth and spread of populations colonizing novel environments. To this end, we need quantitative models that describe invasion mechanistically as the outcome of local growth and dispersal (Williamson, 1996; Shigesada & Kawasaki, 1997; Fagan *et al.*, 2002; Lockwood *et al.*, 2007).

Mechanistic models of invasion are rooted in ecological models of population dynamics in uniform continuous environments, in which invasion patterns are captured by traveling wavefronts moving at constant velocity, or ‘invasion speed’ (Skellam, 1951; Okubo, 1980; Hastings *et al.*, 2005). However, the prediction of invasion continuous waves and constant invasion speed does not square with all biological data (Andow *et al.*, 1990; Holt *et al.*, 2005). Suspected causes of discrepancy include spatial and/or temporal variation in the abiotic environment, environmental and demographic stochasticity, non-Brownian dispersal, Allee effects, and interspecific interactions (Kot *et al.*, 2004; Shigesada *et al.*, 1986; Neubert *et al.*, 2000; Petrovskii *et al.*, 2002, 2005; Caswell *et al.*, 2011; Schreiber & Ryan, 2011; Dwyer & Morris, 2005; Sullivan *et al.*, 2017). Here, we examine the hypothesis that rapid local adaptation and dispersal evolution can, through eco-evolutionary feedbacks (Kokko & López-Sepulcre, 2007; Schoener, 2011; Travis *et al.*, 2014; Metz *et al.*, 1992), play a significant role in shaping the dynamics of population expansion and variation in invasion speed.

Rapid evolution has been demonstrated empirically in colonizing populations, including local adaptation to new habitats (Dlugosch & Parker, 2008; Colautti & Lau, 2015), the evolution of geographic clines along climatic gradients (Huey *et al.*, 2000; Colautti & Barrett, 2013), and the evolution of dispersal ability (Phillips *et al.*, 2006; Lombaert *et al.*, 2014). To investigate the causal role of evolution in population expansion, theory has been developed to address local adaptation on the one hand, and dispersal evolution on the other. In temporally constant environments, quantitative genetics models of local adaptation along environmental gradients (Kirkpatrick & Barton, 1997) predict wave-like patterns of continuous expansion at a constant speed. Given the environmental gradient steepness, dispersal reduces invasion speed due to a negative interaction with local adaptation through gene flow at the expansion edges (Barton, 2001; García-Ramos & Rodríguez, 2002). This ‘standing load’ is potentially aggravated by the ‘expansion load’ created by deleterious alleles ‘surfing’ at high frequency at the expansion edge (Excoffier & Ray, 2008; Hallatschek & Nelson, 2008; Peischl *et al.*, 2015).

Dispersal, however, fuels genetic variation and numerical abundance at the expansion edge (Gomulkiewicz *et al.*, 1999; Holt, 2003), thus alleviating some of the maladaptive effects that limit population spread (Holt & Keitt, 2005; Holt *et al.*, 2005; Alleaume-Benharira *et al.*, 2006; Bridle *et al.*, 2010; Polechova, 2018). Individual variation in dispersal may also result in the ‘spatial sorting’ of high-dispersal individuals at the edge of expansion, which can accelerate invasion (Phillips *et al.*, 2010b; Shine *et al.*, 2011; Bouin *et al.*, 2012). The effect of dispersal variation on invasion

34 speed will be further modulated by the individual fitness cost of dispersal (Ronce, 2007; Burton *et al.*, 2010; Bonte
35 *et al.*, 2012; Clobert *et al.*, 2012) and the response of dispersal to selection, which is expected to vary from the core
36 to the moving edge of the expansion (Dytham, 2009; Kubisch *et al.*, 2014).

37
38 Given their multiple and conflicting effects on population expansion, the joint influence of local adaptation and
39 dispersal variation on invasion dynamics remains poorly understood (Kubisch *et al.*, 2014; Polechova, 2018). This raises
40 the need to extend current theory of species' range and invasion dynamics and take into account the reciprocity between
41 ecological processes and evolutionary change (Kubisch *et al.*, 2014). Specifically, we construct an eco-evolutionary
42 model of invasion dynamics that integrate local adaptation with key factors of dispersal evolution (Hamilton & May,
43 1977; McPeck & Holt, 1992; Cadet *et al.*, 2003; Ronce, 2007; Clobert *et al.*, 2012). Our baseline model is derived from
44 Champagnat & Méléard (2007) eco-evolutionary model of local adaptation, that we extend to include the evolution of
45 dispersal. The original model (without dispersal evolution) predicted the long-term population spatial distribution to
46 be of one of two kinds, either continuous, or clustered (Champagnat & Méléard, 2007; Leimar *et al.*, 2008). Population
47 clustering refers to individuals forming high-density groups interspersed with low density areas (Hassell & May, 1974;
48 Hassell *et al.*, 1990; Niwa, 1994; Flierl *et al.*, 1999; Young *et al.*, 2001). Here we examine how the continuous/clustering
49 dichotomy affects the transient regime of population spread. We show that dispersal evolution interacting with local
50 adaptation drives a generic pattern of invasion shaped by both continuous expansion and population clustering.
51 This pattern is also associated with strong temporal variation in invasion speed, with invasion pulses occurring as a
52 consequence of eco-evolutionary feedbacks between local adaptation and dispersal on the invasion front.

53 **Materials and Methods**

54 **Models**

55 We use an individual-based stochastic model of spatial eco-evolutionary dynamics which was first introduced in
56 Champagnat & Méléard (2007). The model describes a population living on a spatial linear environmental gradient;
57 in its baseline form, only one dimension of space is considered. Each individual is characterized by its physical
58 location x and two quantitative phenotypic traits: a niche position trait along the environmental gradient, u , and a
59 trait measuring individual mobility (or dispersal), w . Individuals give birth asexually at a rate which depends on how
60 adapted they are to their local environment; the difference between the niche position trait and the local optimum
61 measures the degree of maladaptation. We refer to the local optimum as the niche position trait for which the birth
62 rate is highest. With proper rescaling we can assume that this trait value is equal to the geographic coordinate, x .
63 Mobility is modeled as a diffusion (random walk) along the spatial axis of environmental variation. Individuals die at
64 a rate which increases with the intensity of local competition and the cost of dispersal. Offspring inherit their parent's
65 traits, unless a mutation occurs, with constant probability and independently between traits. Mutations are assumed

to have small effects, which may alter the niche trait or dispersal. For simplicity, our model assumes equal mutation probability and mutational variance for both traits.

More precisely, the birth rate B of an individual with niche position u at location x , is given by: $B(x, u) = \max\{b_0 - b_1(x - u)^2; 0\}$. The smooth continuous variation of the maximum birth rate along the line $x = u$ represents the environmental gradient. For instance, if the physical axis represents oceanic depth (Ingram, 2011), $x > u$ corresponds to individuals with niche position u being adapted to shallower waters than their current depth x . Individual dispersal is measured by $D_m w$, where D_m is the intrinsic (constant) dispersal rate and w is the evolving investment in mobility. The death rate of an individual is given by the sum of a density-independent component, equal to $d_0(1 + w)^\theta$ where θ scales the cost of dispersal, and the cumulative (additive) competition effect resulting from interaction with all individuals within a distance δ , the ‘interaction range’, irrespective of their phenotype.

By taking a large-population limit on the individual-based stochastic model, we obtain the following deterministic approximation, which takes the form of an integro-partial differential equation (Champagnat & Méléard, 2007):

$$\begin{aligned} \frac{\partial n(x, u, w, t)}{\partial t} = & D_m w \frac{\partial^2 n(x, u, w, t)}{\partial x^2} + n(x, u, w, t) \times \\ & \left((1 - 2\gamma)B(x, u) - d_0(1 + w)^\theta - \int_{\mathcal{X}} \int_{\mathcal{U}} \int_{\mathcal{W}} \mathbb{1}_{|x-y| < \delta} n(y, a, b, t) db da dy \right) \\ & + \gamma \int_{\mathcal{U}} n(x, a, w, t) B(x, a) \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(u-a)^2}{2\sigma^2}\right) da \\ & + \gamma \int_{\mathcal{W}} n(x, u, b, t) B(x, u) \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(w-b)^2}{2\sigma^2}\right) db, \end{aligned} \quad (1)$$

where (heuristically) $n(x, u, w, t)$ is the density of the population of individuals with niche trait u and dispersal trait w located at x at time t . $\mathcal{U}$, $\mathcal{W}$ and $\mathcal{X}$ denote the ranges of variation of trait u , dispersal w , and location x . Parameters γ and σ^2 are the mutation probability and mutational variance, respectively. In Section S1 of the Supporting Information, we provide more details about the individual-based stochastic process (simulation algorithm) and the deterministic model (boundary conditions, numerical solving scheme).

Results

The deterministic model provides a good approximation of the invasion dynamics generated by the individual-based stochastic process (Section S1.2). In the absence of genetic variation in the niche trait, population expansion is prevented altogether, due to the inability of the species to maintain viable populations in geographic areas where optimal conditions are too different from its original niche (see Section S3). With genetic variation in the niche

92 trait, invasion occurs. As anticipated from Leimar *et al.* (2008), spatial expansion does not necessarily develop as a
93 continuous wave. Local adaptation can shape invasion through the formation of population clusters (Figs 1 and 2).

94
95 At low dispersal (Figs. 1A, 2A), population expansion is ‘pulled’ by clusters forming sequentially, in both spatial
96 and niche trait space, with new clusters adapting gradually to the newly colonized environment (Figs. 1A, 2E). Each
97 new cluster is seeded predominantly by dispersers from previous outer clusters, at the edge of the distribution. (See
98 Sections S2 and S6.3 for the effect of interaction range, mutational variance, gradient steepness and spatial spread of
99 the initial population on cluster formation.)

100
101 If dispersal is above a ‘clustering threshold’, invasion proceeds as pushed by an expanding wave (Figs. 1B-1C, 2B-2C).
102 Edge adaptation to the optimum niche is initially poor and gradually improves (Fig. 2F, 2G). For dispersal above
103 but close to the clustering threshold, the wave is unstable and the distribution breaks out into clusters (Figs. 1B,
104 2B). Here the model shows that it is possible for organisms to invade in continuous waves and yet develop patchy
105 distributions as they spread more broadly.

106
107 For dispersal further above the clustering threshold (Figs. 1C, 2C), wave-like invasion leads to a continuous distribution
108 (Section S2), but adaptation lagging behind spatial spread results in peaks of abundance whose relative position moves
109 during invasion: initially located at the introduction focus, relatively far from the expansion edge (Fig. 1C, $T = 40$);
110 then moving progressively towards the edge (Fig. 1C, $T = 60, 80$). Thus, peaks of invaders’ abundance move outward
111 within the population distribution during expansion, in contrast with non-monotonous waves of invasion with invaders
112 consistently concentrated at the front (*e.g.* Fronhofer & Altermatt (2015)).

113
114 Finally, for very high dispersal (Figs. 1D, 2D), colonization of the whole available space is possible, in a wave-like
115 pattern, even without significant local adaptation during the invasion process. Thus, high dispersal from a focal
116 population well adapted to the introduction site makes spatial spread very rapid, even though most of the population
117 remains maladapted during expansion.

118
119 Invasion speed can vary dramatically in the course of population expansion. At low dispersal (Figs. 2A, 2E, 2I), there
120 is a first, latent phase of invasion during which the population focus spreads only locally and local maladaptation
121 remains low. This is followed by the first invasion pulse, which corresponds to the establishment and growth of the
122 first cluster; at that point invasion stops (Fig. 2I) while the cluster adapts (Fig. 2E). As local adaptation increases,
123 the cluster grows locally and generate enough pioneer dispersers to reach areas of low competition, thus triggering the
124 formation of the next cluster. The process of cluster formation repeats itself, and invasion speed fluctuates between
125 a constant high value and zero.

For higher dispersal (Figs. 2B, 2F, 2J and 2C, 2G, 2K), dispersal is responsible for a first phase of rapid invasion, which turns out to be the fastest (Fig. 2B, 2J and 2C, 2K). Strong maladaptation at the population edge builds up rapidly during this initial phase (Fig. 2F, 2G), which causes invasion speed to drop (Fig. 2J, 2K). Once the population edge is sufficiently adapted, invasion resumes. Invasion speed rapidly reaches a plateau in the case of continuous expansion (Fig. 2C, 2K) or increases gradually in the case of expanding waves breaking down in clusters. At very high dispersal (Fig. 2D, 2H, 2L), expansion into the whole spatial domain occurs very rapidly; local adaptation is much slower (Fig. 2D, 2H), and eventually results in the divergence of niche traits toward extreme values (Fig. 2D).

We can gain further insights into the cluster formation regime by using a Hamilton-Jacobi approximation approach (Diekmann *et al.*, 2005), valid for populations with low dispersal and small mutational variance of the niche trait. We find that the inter-cluster distance is closely approximated by the competition range (Section S5.2). Remarkably, clusters influence one another as they grow and adapt. As a new cluster establishes at the edge, adaptation of the previous front cluster slows down (Fig. 3, blue curve when red cluster appears). This is due to the fact that the formerly front cluster now receives a flow of locally maladapted dispersers from the core and the (new) edge of the range. When combined with sufficient dispersal, these large scale, inter-cluster effects contribute to fluctuation (and possibly increase) of invasion speed found in the case of a fragmenting expansion wave (Fig. 2B, 2J). We also note that for not too small dispersal, where cluster formation occurs yet the Hamilton-Jacobi approximation may not apply, multi-stability is possible (Sections S2 and S4.1). Thus, we expect some quantitative differences in invasion dynamics resulting from the dynamical uncertainty.

We now turn to the case where niche and dispersal evolve jointly. Increasing the cost of dispersal results in a lower clustering threshold on dispersal (Fig. 4). Thus, clustering always occurs, irrespective of the cost of dispersal, provided dispersal is low enough; and in populations experiencing a relatively low cost of dispersal, clustering occurs over a broad range of dispersal rates.

With both niche and dispersal traits evolving, mean dispersal always tends to decrease (Fig. 5A-5C). However, if the dispersal rate of ancestral colonizers is far enough (above or below) from the clustering threshold, the selection gradient against dispersal is weak (Fig. 5B). Thus, three alternate patterns of spatial expansion and invasion dynamics emerge. If ancestral dispersal is below the clustering threshold, the population expands through cluster formation (Fig. 5A, 5D, 5G, 5J). If ancestral dispersal is far above the clustering threshold, the population expands as a continuous wave (Fig. 5B, 5E, 5H, 5K). For intermediate dispersal values, the evolution of dispersal drives the population across the clustering threshold, causing the invasion regime to shift from continuous to clustering (Fig. 5C, 5F, 5I, 5L). For colonizing populations of highly mobile individuals introduced in a new environment that is sufficiently vast, the latter scenario is expected generically.

162 A broad range of dispersal trait values evolve in the course of the invasion (Fig. 5A-5C). In spite of dispersal being
 163 selected against, even at the invasion front (Fig. 5G-5I), there is always ‘spatial sorting’ (Shine *et al.*, 2011) at the
 164 population edge (Fig. 5D-5F). In addition, in the case of clustering expansion, mean dispersal and the degree of local
 165 (mal)adaptation, both measured in the front cluster, vary through time (Fig. 5G, green curve for dispersal, blue
 166 curve for local maladaptation). Every time a new cluster forms, mean dispersal reaches a higher value (because of
 167 high-dispersal individuals coming from inner clusters further away from the edge) while local maladaptation is reset
 168 to a relatively constant level; as the new cluster grows, both mean dispersal and the degree of local maladaptation
 169 drop lower than they did in the previous front cluster.

170
 171 Dramatic variation of invasion speed can occur (Fig. 5J, 5K, 5L). Dispersal evolution driving invasion from wave-like
 172 to clustering causes an abrupt shift in invasion speed, from being relatively constant to fluctuating widely (Fig. 5L).
 173 In the clustering regime of invasion, invasion speed tends to increase between consecutive pulses of expansion (Fig.
 174 5J). This means that each new front cluster grows faster than the previous one. This is somewhat unexpected given
 175 that mean dispersal in the front cluster increases (Fig. 5G, green curve), hence a larger demographic cost, while the
 176 level of maladaptation remains about the same across new front clusters (Fig. 5G, blue curve). In fact, a new front
 177 cluster is a mix of individuals that come potentially from all inner clusters. Those individuals that come from near
 178 clusters have relatively low dispersal rates (hence a low cost of dispersal) and are less maladapted as they move up
 179 front; their birth rate is therefore relatively high. Every time a new front cluster forms, the former front cluster is
 180 less maladapted than the previous one (*cf.* blue curve dropping deeper in Fig. 5G). As a consequence, individuals
 181 that move from the former front cluster, have higher fitness compared to individuals that made similar moves on a
 182 previous event of front cluster formation, hence the increase in invasion speed.

183
 184 The inclusion of Allee effects does not change the overall pattern: cycles of accelerating-decelerating invasion, existence
 185 of a clustering threshold on dispersal, and selection against dispersal that drives a rapid transition from wave-like to
 186 clustered invasion (Fig. 6, Sections S1.3, S6.4 and S6.5). Allee effects also favor clustering (lower clustering threshold,
 187 for any given cost of dispersal). In agreement with existing theory, Allee effects tend to slow down invasion, and in
 188 the wave-like regime of population with expansion (Figs. 6B), the invading wave is ‘pushed’ rather than ‘pulled’.
 189 As a consequence, mean dispersal on the front is lower than in the rest of the range (Figs. 6E). In contrast, in the
 190 clustering regime of invasion, expansion is pulled by new clusters, where spatial sorting of high-dispersal individuals
 191 followed by selection against dispersal occur (Figs. 6G), as in the case without Allee effects.

192 Discussion

193 Local adaptation and dispersal evolution are key evolutionary processes shaping the invasion dynamics of populations
 194 colonizing new environments (Dlugosch & Parker, 2008; Colautti & Lau, 2015; Lambrinos, 2004; Stockwell *et al.*,

2003; Phillips *et al.*, 2006). To resolve their interaction, we use a simple eco-evolutionary model of a single-species population along a one-dimensional resource gradient. The predicted long-term spatial distribution of the population (continuous or clustered) has major consequences on the invasion dynamics. Below a threshold (*clustering threshold*) on the dispersal rate of initial colonizers, invasion develops in pulses, driven by bouts of spatial sorting and local adaptation. For colonizers with dispersal above the threshold, the generic pattern of invasion begins with a phase of acceleration-deceleration, continues as a wave traveling at constant speed, until selection against dispersal drives an abrupt transition into the pulsed regime of invasion. Whereas our model constraints spatial dynamics to one dimension of environmental variation, similar dynamics occur if we unfold a second spatial dimension and let dispersal occur in both directions (Section S6.1).

The finding of long-term population spatial distribution being either continuous (for dispersal above a threshold) or clustered (for dispersal below a threshold) is similar to Leimar *et al.* (2008), but our model differs in three ways: First, rather than limiting individual mobility to dispersal at birth, we assume that individuals can change location throughout their life. Intuitively, this favors mixing and sets a priori more restrictive conditions for cluster formation. Second, we use competition kernels that are box-shaped rather than Gaussian. This removes spurious effects of Gaussian competition kernels (Roughgarden, 1972, 1979; Metz *et al.*, 1995; Leimar *et al.*, 2008). Third, we exclude fitness frequency-dependence from our assumptions, by assuming that competition intensity does not depend on relative trait values. Even though we define competition with respect to physical location, the interplay between competition with neighbors and local adaptation results in a correlation between physical location and trait, which can lead to fragmentation in both dimensions (Leimar *et al.*, 2008). Compared to Leimar *et al.* (2008), we found a broader range of dispersal and other parameter values for which clustering is expected, which is explained by our stability analysis accounting for perturbations in both space and trait dimensions. Allee effects further enlarge the range of conditions for clustering. Similarly to Leimar *et al.* (2008) we find that population clustering is promoted by intermediate gradient steepness. Recent mathematical work backs up the generality of long-term clustering as an outcome of competition within neighborhoods (Alfaro & Coville, 2012; Han & Zheng, 2016).

Dispersal evolution plays a key role in driving the invasion regime from wave to clusters. In general, dispersal evolution is shaped by a set of costs and benefits (reviewed *e.g.* in Ronce (2007); Duputié & Massol (2013)). Costs of dispersal include intrinsic costs, and environmentally-mediated costs (how risky movement is, and the fitness loss due to moving away from areas to which the population is adapted or into habitats of low quality). Benefits of dispersal include the potential to found new population where competition is released, avoidance of kin competition, and in sexual organisms, inbreeding avoidance. In temporally constant, spatially heterogeneous environments, dispersal is generally selected against (Hastings, 1983; Hutson *et al.*, 2003; Cantrell *et al.*, 2009; Bolker, 2010; North *et al.*, 2011), unless there are mechanisms to counter the risk of fitness loss due to spatial heterogeneity, such as conditional dispersal (Cantrell *et al.*, 2006) or local adaptation (Billiard & Lenormand, 2005; Blanquart & Gandon, 2014). The organisms'

life cycle is also a strong influence of selection on dispersal; evolution of dispersal in the adult stage (as in our model) generally involves more stringent conditions on environmental structure and variation (Massol & Débarre, 2015).

Costs and benefits of dispersal can vary across a species' range, and may be particularly large at the range margins, where dispersers can reach previously unoccupied areas but face Allee effects and genetic drift (Holt, 2003; Excoffier & Ray, 2008; Dytham, 2009). Previous theory has explored the evolution of dispersal as a population expands across a spatially homogeneous environment (*e.g.* Travis & Dytham (2002); Travis *et al.* (2009)) or across an environmental gradient (Kubisch *et al.*, 2010). How selection acts on dispersal during periods of range expansion can be very different from selection on dispersal in stationary populations (Travis *et al.*, 2009). On an expanding front, dispersal may be strongly favored because of spatial sorting and selection (Travis & Dytham, 2002; Phillips *et al.*, 2008; Shine *et al.*, 2011), despite spatial heterogeneity acting against dispersal on average across the range (Travis *et al.*, 2009; Bartoń *et al.*, 2011). Spatial sorting refers to the fact that the best dispersers tend to be disproportionately represented on the population front; competition release experienced by these individuals may result in larger reproductive success, hence selection for increased dispersal.

In addition to spatial sorting and selection, kin competition may also be a strong agent of selection on dispersal at the population front, because founder effects driving invasion result in locally high relatedness (Cote *et al.*, 2007; Kubisch *et al.*, 2013). For invasion occurring along spatial gradients of resources, kin selection for dispersal may counter the cost of maladaptation incurred by dispersers (Kisdi, 2002; Billiard & Lenormand, 2005). Blanquart & Gandon's (2014) analysis suggests that the balance of kin selection and maladaptation is determined by the strength of intraspecific competition and the intrinsic cost of dispersal (which influence local population size), and the gradient steepness (which influences the spatial variance in selection on resource use).

In our model, several selective agents act against dispersal: the intrinsic mortality cost; spatial heterogeneity manifested in the gradient of resources, and enhanced by population self-structuring when dispersal is close to or below the clustering threshold; and the cost of maladaptation. Selection against dispersal is particularly strong around the clustering threshold. If the ancestral phenotype is above the threshold, the eco-evolutionary feedback on dispersal can drive a macroscopic transition from wave-like to pulsed invasion: as spatial population heterogeneity develops when dispersal becomes sufficiently close to the threshold, selection against dispersal intensifies; lower dispersal enhances spatial variation in population density, thus selecting even more strongly against dispersal, which eventually crosses the clustering threshold.

We found that spatial sorting generally occurs, but not spatial selection. High-dispersal individuals tend to be assorted at the range margin (front cluster or wave front), but the benefit of low density (reduced competition) and kin selection appear to be too weak to counter maladaptation, resulting in selection against dispersal ('suppressed spatial selection')

Perkins *et al.* (2013)). In the wave-like invasion regime, suppressed spatial selection leads to invasion occurring at constant speed (past the initial phase of acceleration-deceleration), rather than accelerating (Phillips *et al.*, 2010a).

In the clustered invasion regime, the consequences of suppressed spatial selection for invasion dynamics are germane to the phenomenon of ‘elastic’ range expansion (Holt, 2003; Kubisch *et al.*, 2010), whereby a population invasion progresses in alternating bouts of expansion and contraction. In our model of clustered invasion, the rapid formation of new front clusters by spatial sorting is followed by a phase of local adaptation and selection against dispersal within clusters. This results in a dynamical pattern of alternating range expansion and pause, rather than contraction. In addition, the speed of expansion bouts tend to increase, reflecting the more rapid growth of newly formed clusters. The accelerating growth of new clusters is driven by a positive feedback with local adaptation in the ‘source’ clusters: colonizers will be less maladapted to their new location on the invasion front, and therefore establish faster-growing populations that will send even less maladapted individuals to form the next front cluster.

Data-model fitting and model selection for the cane toads case (Phillips *et al.*, 2006, 2010a) has provided strong support for spatial selection on dispersal causing an accelerating invasion (Perkins *et al.*, 2013). However, the scope of the mechanism remains to be determined. Mathematical analyses of ‘cane toad equations’ have assumed homogeneous environments, no cost of dispersal, and ‘point local’ competition (Benichou *et al.*, 2012; Bouin *et al.*, 2012), which limits their relevance to real systems. Fitness costs of dispersal (Bonte *et al.*, 2012) influence the dynamics of range expansion (Burton *et al.* (2010); this work), as the form and spatial structure of density regulation does too (Filin *et al.* (2008); this work). Recent experimental work on laboratory systems sought out to evaluate the effect of spatial evolutionary processes on invasion (Williams *et al.*, 2016; Ochocki & Miller, 2017; Szűcs *et al.*, 2017; Fronhofer & Altermatt, 2015). For populations exposed to a novel environment, Szűcs *et al.* (2017) showed that expansion and invasion speed were strongly influenced by local adaptation, whereas spatial evolutionary processes acting at the edge contributed less, which is consistent with our predictions. Specific predictions from our model, such as changes in expansion regime and concurrent variation in invasion speed, could be tested by setting up microcosm experiments on environmental gradients and artificially varying interaction range and gradient steepness.

From a genetic point of view, range expansion usually leads to decreasing genetic diversity, either affecting adaptation (Excoffier *et al.*, 2009) or dispersal (Cobben *et al.*, 2015). The dynamics of genetic diversity at the margins of an expanding range can differ markedly between pulled *vs.* pushed waves (Roques *et al.*, 2012; Garnier & Lewis, 2016). In pulled waves, competition is relaxed on the front, where ‘pioneer’ individuals filtered by spatial sorting can establish growing populations. Thus, the wave travels through recurrent founding events, and genetic diversity is consistently low on the front. With Allee effects, pioneer individuals are less likely to establish front populations that pull the wave; instead the wave is pushed by the growth of populations at the back of the front, and no genetic diversity is lost on the front (Roques *et al.*, 2012). In our model, the same effect is predicted in the case of wave-like invasion (Fig.

5B, E; Fig. 6E). The model predictions differ when clustering occurs. In this case, invasion is pulled by new clusters even when Allee effects operate (Fig. 6A, D, G). In contrast, Allee effects prevent new clusters to form from the population low-density ‘nose’ ahead of the core even though competition is relaxed. Instead, new clusters must form through spatial sorting of high-dispersal individuals, causing a founder effect. Thus genetic diversity is reduced, but eventually rebuilds by mutation, which fuels local adaptation of the newly formed cluster. How fast genetic variance of both dispersal and niche traits builds up depends on the mutation rates, which thus appear as key parameters of the invasion dynamics in the clustering regime.

Conclusions

In contrast with long-standing theory predicting that, under a wide range of conditions, a population will asymptotically spread with a constant velocity (Skellam, 1951; Okubo, 1980), there has been growing empirical evidence that invasion speed can be variable (Johnson *et al.*, 2006; Melbourne & Hastings, 2009; Chen, 2014; Ochocki & Miller, 2017; Weiss-Lehman *et al.*, 2017). Empirical studies often attributed temporal variation in invasion speed to differences in the environments encountered by the invading population (Andow *et al.*, 1990; Peltonen *et al.*, 2002), while models pointed to potential endogenous factors, such as demographic stochasticity causing time lags in population expansion (Sakai *et al.*, 2001; Snyder & Ives, 2003; Liebhold & Tobin, 2006), and long-distance dispersal (Shigesada *et al.*, 1995; Kot *et al.*, 1996) or Allee effects (Keitt *et al.*, 2001; Petrovskii *et al.*, 2002, 2005; Johnson *et al.*, 2006) driving pulsed invasion.

Our model offers an alternate mechanism for lags in expansion and pulsed invasion, based on the interaction of dispersal evolution and local adaptation along an environmental resource gradient. For dispersal below the clustering threshold, invasion accelerates when high-dispersal individuals are spatially sorted on the population front, and pauses as the front clusters adapts to the newly colonized habitat. Selection driving dispersal across the clustering threshold will cause an abrupt transition from wave-like invasion at constant speed to the clustering regime of pulsed invasion. The interaction range, cost of dispersal, and genetic variance of niche and dispersal traits, thus arise as key factors of the dynamics of invasion, in addition to gradient steepness (Leimar *et al.*, 2008; Polechova, 2018).

How often and to what extent do eco-evolutionary processes affect invasion dynamics in nature, given the pervasive influences of environmental heterogeneity and demographic stochasticity and their roles in invasion variability? To begin to answer this question, we suggest that coupling models and empirical data, as was done in Perkins *et al.* (2013), is a promising approach. The power of model-data integration will be enhanced by further theoretical developments to address other important factors of population spread, including resource-consumer interactions (Holt *et al.*, 2011; Kubisch *et al.*, 2014; Fronhofer & Altermatt, 2015), conditional dispersal (Dwyer & Morris, 2005; Travis *et al.*, 2009;

333 Sullivan *et al.*, 2017; Liu *et al.*, 2016), and selection on multiple life-history traits (Kanarek & Webb, 2010; Burton
334 *et al.*, 2010; Perkins *et al.*, 2013).

335 Competing interests

336 We declare we have no competing interests.

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Figure 1: *Spatial eco-evolutionary dynamics of invasion with local adaptation and constant dispersal. Time-evolution of the population distribution. A. $D_m = 5 \times 10^{-5}$. B. $D_m = 8 \times 10^{-5}$. C. $D_m = 5 \times 10^{-4}$. D. $D_m = 2 \times 10^{-2}$. At $T = 0$ the distribution is Gaussian with standard deviation $\sigma_0 = 0.1$ (in both dimensions) centered at $(0.5, 0.5)$. Large-population model given by Eq. (S2), parameters set to the default clustering values in Table S2. In all panels cyan represents the lowest density and magenta the highest. Density is negligible in white areas.*

Figure 2: *Spatial eco-evolutionary dynamics of invasion with local adaptation and constant dispersal. Time-evolution of spatial and niche-trait distributions for $D_m = 5 \times 10^{-5}$ (Panel A), $D_m = 8 \times 10^{-5}$ (Panel B), $D_m = 5 \times 10^{-4}$ (Panel C), $D_m = 2 \times 10^{-2}$ (Panel D). Time-evolution of local maladaptation, measured by the distance between the local optimum and physical location ($|x - u|$) at the population front for $D_m = 5 \times 10^{-5}$ (Panel E), $D_m = 8 \times 10^{-5}$ (Panel F), $D_m = 5 \times 10^{-4}$ (Panel G), $D_m = 2 \times 10^{-2}$ (Panel H). Front invasion speed for $D_m = 5 \times 10^{-5}$ (Panel I), $D_m = 8 \times 10^{-5}$ (Panel J), $D_m = 5 \times 10^{-4}$ (Panel K), $D_m = 2 \times 10^{-2}$ (Panel L). At $T = 0$ the population distribution is Gaussian with standard deviation $\sigma_0 = 0.1$ (in both dimensions) centered at $(0.5, 0.5)$. Large-population model given by Eq. (S2), other parameters set to the default clustering values in Table S2. In all panels cyan represents the lowest density and magenta the highest. Density is negligible in white areas.*

Figure 3: *Spatial eco-evolutionary dynamics of invasion with local adaptation and constant dispersal: dynamics of cluster emergence and adaptation. Simulation based on the Hamilton-Jacobi equation Eq. (S16). Time-evolution of adaptation, measured by angular degree between the cluster alignment and gradient (cf. Fig S15). T_i , $i = 1, 2, 3$, indicate times at which new clusters emerge. Parameters set to the default clustering values in Table S2.*

Figure 4: *Influence of dispersal value and cost on long-term spatial population structure. The bifurcation line between clustering and continuous spread is computed as the zero contour of the Lyapunov exponent given by Eq. (S6). Large-population model given by Eq. (1). Other parameter values are set to the default parameter values in Table S1.*

Figure 5: *Spatial eco-evolutionary dynamics of invasion with local adaptation and evolving dispersal. (A-C) Time-evolution of spatial, niche-trait and dispersal-trait distributions. (D-F) Local mean dispersal as a function of spatial location. (G-I) Time-evolution of local maladaptation at the population front, measured by the distance between the local optimum and physical location ($|x - u|$), and mean dispersal at the population front. (J-L) Time-evolution of invasion speed. Large-population model given by Eq. (1). At $T = 0$ the population distribution is Gaussian with standard deviation $\sigma_0 = 0.1$ (in the three dimensions) centered at $(0.5, 0.5, w_0)$. Parameter values: $w_0 = 0.15$ and $\theta = 0.75$ in A, D, G, J; $w_0 = 0.9$ and $\theta = 0.75$ in B, E, H, K; $w_0 = 0.3$ and $\theta = 1.75$ in C, F, I, L. Other parameters set to the default values in Table S1. In Panels A, B and C, cyan represents the lowest density and magenta the highest. Density is negligible in white areas.*

Figure 6: *Spatial eco-evolutionary dynamics of invasion with local adaptation, evolving dispersal, and Allee effect (Section S1.3). Large-population model given by Eq. (1). See Fig. 5 for panel labeling and other details.*