CHICAGO JOURNALS

American Society of Naturalists

The University of Chicago

Note

Kin Competition as a Major Driving Force for Invasions

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abstract: Current theory explains accelerating invasions with increased levels of dispersal as being caused by "spatial selection." Here we argue that another selective force, strong kin competition resulting from high relatedness due to subsequent founder effects at the expanding margin, is of at least comparable importance for dispersal evolution during invasions. We test this hypothesis with individual-based simulations of a spatially structured population invading empty space. To quantify the relative contribution of kin competition to dispersal evolution, we contrast two scenarios, one including kin effects and one excluding them without influencing spatial selection. We find that kin competition is a major determinant for dispersal evolution at invasion fronts, especially under environmental conditions that favor a pronounced kin structure (i.e., small patches, low environmental stochasticity, and high patch isolation). We demonstrate the importance of kin competition and thus biotic influences on dispersal evolution during invasions.

Keywords: invasion, spatial selection, kin competition, dispersal evolution, range dynamics, individual-based model.

Introduction

Species invasion is recognized to be a major threat to current biodiversity and is expected to strongly increase in frequency under the spell of global climate change (Shigesada and Kawasaki 1997; Prentis et al. 2008; Walther et al. 2009; Bradley et al. 2011). Dispersal is the key mechanism responsible for colonization of new habitats and, consequently, is the dominant process underlying such invasions (Cote et al. 2007; Wilson et al. 2009). However, dispersal is known to be a highly plastic and rapidly evolving trait, which is a fact that challenges our understanding of invasion processes (Parmesan 2006; Alford et al. 2009; Travis et al. 2009).

Indeed, an often-documented phenomenon during invasions is an accelerating rate of range expansion emerging over time. This has usually been attributed to an increase in the dispersiveness of marginal populations, which is a tendency observed in many systems, including birds (Duck-

worth 2008), insects (Hill et al. 1999; Thomas et al. 2001; Simmons and Thomas 2004), and the well-studied cane toads in Australia (Phillips et al. 2008; Urban et al. 2008).

The phenomenon has also attracted the interest of some theoretical investigations (Burton et al. 2010; Kubisch et al. 2010; Travis et al. 2010). The most common explanation for the emergence of the phenomenon relies on a simple ecological filter effect, termed "spatial sorting" or "spatial selection" (Phillips et al. 2010b; Shine et al. 2011). Like athletes in a footrace, the most mobile and dispersive individuals form the front of an expanding population. Given a high heritability of dispersal strategies, the most dispersive genotypes will thus accumulate in habitats at the range front, thus speeding up the likelihood of colonizing additional unoccupied habitat. This spatial selection process has indeed been studied intensively. In cane toads, for example, the effect is not only plastic but seems to have an underlying genetic basis (Phillips et al. 2010a). Spatial selection might even offer an explanation for the formation of stable range boundaries during range expansion into gradient systems (Phillips 2011).

Because the mechanism underlying spatial selection is very obvious and convincing, it is tempting to explain the increasing dispersiveness during invasions exclusively by this mechanism. However, at least two additional processes have the potential to also result in selection for higher emigration rates and dispersal distances close to range margins. First, the chance to colonize empty habitat is very high for migrants from marginal areas. In newly established, low-density populations, the direct fitness of colonizers is increased compared with that of individuals in established populations. However, the colonizers' descendants (who are located in areas where high dispersal is the most beneficial strategy) will also have an advantage from this reduced competition, as long as population size has not reached carrying capacity. This implies a multigenerational benefit for highly dispersive individuals at the range margin. In a simulation study exploring the evolution of density-dependent emigration during invasions, Travis et al. (2009) have already demonstrated that such long-term benefits outweigh the short-term fitness disadvantages of dispersing individuals.

Second, kin competition may be another mechanism to explain the observed dispersal increases, as has been proposed by Cote et al. (2007). Kin competition is known to be an important driver for dispersal evolution (Hamilton and May 1977; Poethke et al. 2007; Ronce 2007) and has been well documented in natural systems (Cote et al. 2007). Given the subsequent founder events occurring at an advancing range front (which also build the basis for spatial selection), we expect that relatedness gradually increases, which implies a growing selective contribution of kin competition. When kin structure becomes more pronounced, higher costs of dispersal can be balanced by these indirect fitness gains (Hamilton and May 1977):

$$\Delta\omega_i + \sum_{j=1}^{N} r_{i,j} \cdot \Delta\omega_j > C, \tag{1}$$

where $\Delta\omega_i$ denotes the resulting benefit for the emigrant through reduced competition in the new patch and $\sum_{j=1}^{N} r_{i,j} \cdot \Delta\omega_j$ is the fitness increase of all other inhabitants N in the natal population due to reduced competition weighted by the relatedness coefficient. If the inclusive benefit of emigration exceeds the costs (C) associated with dispersal, emigration is selected for.

In our study, we focus on the contribution of increasing kin competition to the evolution of increased dispersal at expanding range margins. Individual-based simulations account for kin competition by default (Bach et al. 2006; Poethke et al. 2007). However, Poethke et al. (2007) developed a method to exclude the effect of kin structure from individual-based models. Below we will use this approach to quantify the relative contributions of spatial selection and kin competition to the evolution of (elevated) dispersal at expanding range margins.

Methods

Landscape and Individuals

We use an individual-based model of a spatially structured population of an insect species with nonoverlapping generations. This approach has been used in various studies before (Travis et al. 1999; Kubisch et al. 2011; Poethke et al. 2011; Fronhofer et al. 2012). The simulated landscape consists of $x \cdot y = 200 \cdot 50$ habitat patches arranged on a rectangular grid. Every patch may contain a subpopulation of the species, assuming a carrying capacity K (see below). At initialization, we filled all patches from $x = 1$ to $x = 50$ with individuals. Dispersal alleles are initially randomly drawn from a uniform distribution between 0 and 1, and alleles at the neutral locus for determination of genetic structure are random numbers between 0 and 100. During a burn-in period of 1,000 generations, dispersal was restricted to these 250 habitat patches by wrapping them also in x-direction, building a torus without edge effects. The purpose of this burn-in phase is to allow for the evolution of a stable dispersal strategy for a metapopulation in equilibrium. Once that phase was over, the dispersal barrier was removed, and the species could start to expand its range. In a part of the simulations, kin structure was destroyed according to the mechanism described above. Local populations consist of individuals, which are characterized by their sex, by two alleles at one locus coding for density-independent emigration propensity, and by two neutral alleles (random integer numbers between 0 and 100) at another locus, which are used to determine the genetic structure (F_{ST}) of the metapopulation (see below).

Population Dynamics

Local population dynamics follow the logistic growth model for nonoverlapping generations developed by Beverton and Holt (1957). We draw the females' average offspring number for every patch and generation $\overline{\Lambda}_{x,y,t}$ from a lognormal distribution with mean $2 \cdot \lambda$ and standard deviation σ, the latter reflecting the magnitude of environmental stochasticity. Afterward, every female in a patch gives birth to a number of offspring drawn from a Poisson distribution with mean $\overline{\Lambda}_{x,y,t}$. Because of density-dependent competition, offspring survive with a certain probability s, which is given by

$$s = \frac{1}{1 + (\lambda - 1)/K \cdot N_{x,y,t}} \tag{2}$$

with K being carrying capacity of a patch and $N_{x,y,t}$ denoting the population size of a focal patch. A newborn individual inherits one randomly selected dispersal allele from its mother and one from a father randomly chosen from the males residing in the same patch, respectively. Alleles may mutate with probability $m = 10^{-4}$ by adding a Gaussian-distributed random number with mean 0 and standard deviation 0.2. If alleles mutate to negative numbers, they result in an emigration probability of 0, and if they get values larger than 1, they result in a probability to emigrate of 1. The sex of any offspring is appointed randomly.

Dispersal

Surviving offspring emigrate with a probability that is calculated as the arithmetic mean of an individual's two dispersal alleles. If an individual disperses, it may die with a certain probability μ. This dispersal mortality includes all costs associated with dispersal, such as predation risk or energetic costs (Bonte et al. 2012). It reflects, for example, mortality risks associated with patch isolation (Kubisch et

al. 2011). If an individual survives the transition phase, it immigrates into one of the eight neighboring habitat patches (i.e., we assume "nearest neighbor" dispersal). To avoid edge effects, we wrap the world in *y*-direction, thus forming a tube along the *x*-dimension of the world (in the core area, individuals leaving the world along the *x*-dimension are reflected).

Removing Kin Competition

To tease apart the effects of spatial selection and kin competition, we exclude kin effects using an approach invented by Poethke and colleagues (2007) to investigate the relative contribution of kin competition on dispersal evolution. Following their method, the number of individuals in each of the 50 patches that share the same *x*-coordinate is recorded after all individuals reach maturity (but before dispersal). Subsequently, all individuals from these patches are collected and randomly redistributed into them with the constraint that the previous population size of each patch is maintained. This procedure is repeated for all 200 different *x*-coordinates. Thus, only the genetic substructure in one column of patches (patches of identical *x*-coordinate) is destroyed, whereas all other factors influencing dispersal evolution (e.g., spatiotemporal heterogeneity) are not affected. By shuffling only between patches that share the same *x*-coordinate (direction or range expansion), the mechanism of spatial selection is also not influenced, thus allowing for a clear separation of the influences of both selective forces. With regard to equation 1, this shuffling algorithm equalizes the relatedness coefficient *r* in all respective patches and thus reduces the indirect benefit of emigration.

Experiments and Analysis

To test the influences of several environmental parameters on the relative contribution of kin competition to dispersal evolution, we performed simulations with different values for carrying capacity ($K \in \{50, 100, 150\}$), per capita growth rate ($\lambda \in \{1.5, 2, 3\}$), the magnitude of environmental stochasticity ($\sigma \in \{0.25, 0.5, 0.75\}$), and dispersal mortality ($\mu \in \{0.15, 0.3, 0.45\}$). The standard (reference) settings were $K = 100$, $\lambda = 2$, $\sigma = 0.5$, and $\mu = 0.3$.

We determined the range border as the position of the farthest occupied patch in invasion direction. Alternative definitions for range borders have been tested but did not lead to different results. Emigration probabilities at the range border were calculated as the mean taken over all individuals in all patches at the five *x*-coordinates closest to the range border.

We also determined the genetic structure of populations in each column by calculating Wright's fixation index F_{ST}

(Wright 1950) on the basis of the two neutral alleles (see "Landscape and Individuals"). Thus, we can directly measure the genetic differentiation between marginal populations. Genetic structure at the range border was calculated as the mean F_{ST} taken over the five columns (*x*-coordinates) closest to the range border. An analysis of identity by descent was also performed to directly investigate relatedness within and between patches, but this analysis led to the same conclusions (results not shown). The speed of invasion (ν) is calculated as the rate of range border displacement over time in *x*-dimension.

We assessed the relative contribution of kin competition Δ_r by calculating the change of marginal emigration rate and speed of invasion when excluding kin competition relative to the control scenario. Equation (2) shows this calculation for the example of marginal emigration rates from the control scenario (e_c) and the scenario without kin competition (e_r). For the absolute values of marginal emigration and invasion speed, see table A1 in the appendix.

$$\Delta_r = \frac{e_c - e_r}{e_c} \tag{3}$$

Results and Discussion

The Impact of Kin Competition on Marginal Emigration and Relatedness

Our simulations show that kin competition is an important driver for species invasions (fig. 1). For the standard scenario, we find a lower invasion speed, when kin competition is excluded from the simulations (reduction of ~30%; fig. 1*A*). This effect can be directly related to the different evolutionary response of emigration probabilities in the two scenarios; we observe a massive increase in marginal emigration probability, from approximately 0.04 to 0.4, at the expanding range margin in the control scenario. This increase is strongly reduced (from 0.04 to ~0.16) for the scenario with kin competition removed (fig. 1*B*). Thus, the increase in emigration probability at range margins is approximately 60% less when kin competition is excluded.

The reason for this outcome becomes apparent when investigating the genetic structure in the marginal area. During the burn-in phase, we find values for F_{ST} of approximately 0.22 (which indicates medium differentiation of populations; for details, see Fronhofer et al. 2012). However, the progression of F_{ST} is then quite different during the invasion phase for the two scenarios (fig. 1*C*). In the control scenario, we observe a drastic initial increase in genetic difference between marginal patches. This is caused by founder effects that lead to an increased relatedness within but considerable genetic difference between pop-
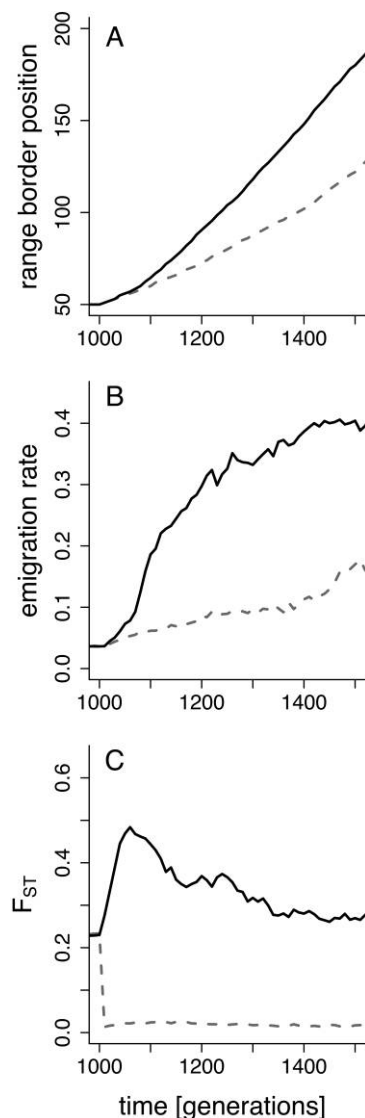
Figure 1: Effect of excluding kin competition for dispersal evolution during invasions for an exemplary simulation run. Shown are change in range border position over time (*A*), emerging emigration rates at range margin (*B*), and mean genetic substructure (*C*; F_{ST}) of the five columns of patches closest to the range border (see "Methods" for details). The black line indicates spatial selection and kin competition, whereas the dashed gray line indicates spatial selection only (kin competition excluded). Standard parameter values used were as follows: $K = 100$, $\lambda = 2$, $\mu = 0.3$, and $\sigma = 0.5$.

ulations. Over time, however, F_{ST} decreases again as emigration rates increase and reduce genetic differentiation between populations. For the scenario with kin structure removed, between patch genetic differentiation (F_{ST}) remains close to zero, because the shuffling of individuals is applied.

These results thus indicate that the high genetic differ-

entiation between patches at range margins emerging in the control scenario strongly contributes to the dispersal benefit, because emigration effectively allows individuals to avoid competition among (close) kin. Clearly, as marginal populations become more equal in their genetic composition over time (because of the repetitive sequence of founder effects), this benefit of dispersal gradually disappears. However, at this time, highly dispersive and (because of the previous selective history) highly monomorphic populations will have formed. Our results thus indicate that the kin-competition-driven phase strongly determines which dispersal strategies ultimately dominate at range margins.

The Relative Contribution of Kin Competition to Invasions in Different Landscapes

Our simulations allow us to also analyze the influence of specific landscape attributes, such as habitat size, quality, or isolation, which are known to impact kin structure (Poethke et al. 2007). These attributes are reflected in our parameters K (i.e., habitat size), λ (i.e., habitat quality), μ (i.e., habitat isolation), and σ (i.e., environmental stochasticity). Results show that the contribution of kin competition depends most strongly on dispersal mortality μ. Carrying capacity K and environmental stochasticity σ also have an impact on the relative influence of spatial selection and kin competition, whereas this relation is rather insensitive to changes in the growth rate λ.

More specifically, we find the highest relative contribution of kin competition to the selection on emigration probabilities (≈ 0.71) and also expansion speed (≈ 0.37) for the smallest tested patch size ($K = 50$; fig. 2*A*). This is not a surprising result, because smaller populations per se imply higher degrees of relatedness. In addition, smaller patch sizes (i.e., smaller effective population sizes and increased demographic stochasticity) strengthen the effects of random genetic drift. This drift tends to reduce diversity of genetic lineages (increase relatedness) within populations and increase between-patch differences, thus strengthening the selective force of kin competition.

Increasing environmental stochasticity leads to a proportional reduction of the influence of kin competition (fig. 2*B*). This effect seems surprising, because one could expect higher stochasticity to reduce effective population size and thus increase kin structure. However, a second process is involved when dispersal evolution is seen in the context of environmental stochasticity. It is well known that fluctuations in population size select for increased dispersal, because they increase the chances to migrate from a high-density to a low-density patch for simple statistical reasons (Cohen and Levin 1991; Cadet et al. 2003; Kubisch and Poethke 2011). In turn, the higher emigration probabilities
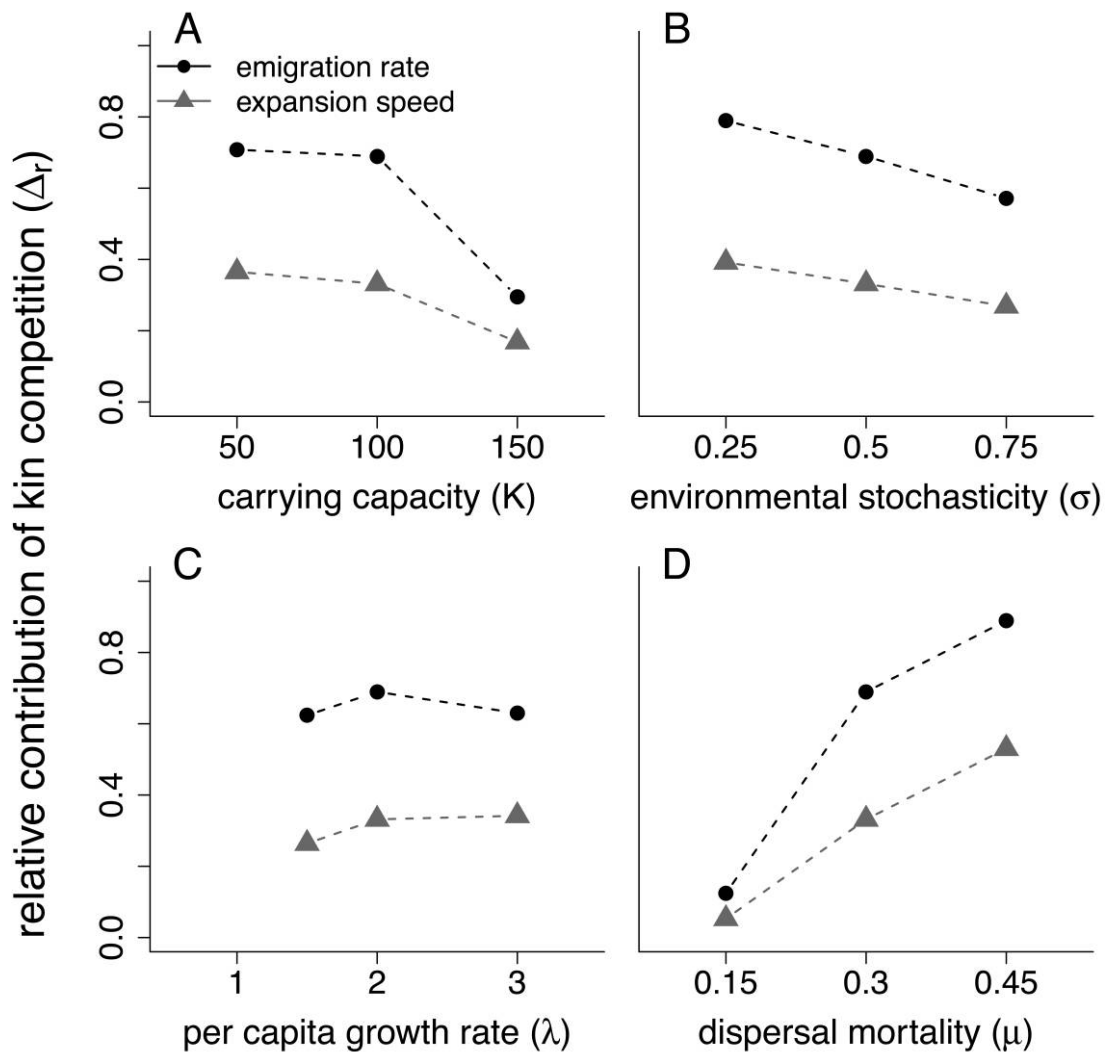
Figure 2: Relative contribution of kin competition to emigration rate (black dots) and speed of range expansion (gray triangles) calculated as the relative difference between values for the scenarios with spatial selection and kin competition and spatial selection only. Plotted are median values for 50 replicate simulation runs for each scenario. Where not indicated otherwise, the following standard values were used for the simulations: $K = 100$, $\lambda = 2$, $\mu = 0.3$, and $\sigma = 0.5$.

evolving under such conditions may result in a lower relatedness because of gene flow between patches and thus lower the influence of kin competition. It is reasonable to assume that the effect of environmental stochasticity on dispersal evolution due to kin competition is weak, because these two opposing mechanisms are acting.

Per capita growth rate has a comparably low impact on both local kin structure and evolving dispersal, especially during the invasion. Thus, it is of minor importance in influencing kin competition, compared with spatial selection (fig. 2C). Changing dispersal mortality, however, has the strongest influence on the contribution of kin competition (fig. 2D). For a high dispersal mortality ($\mu =$

0.45), approximately 89% of change in dispersal and 53% of the acceleration in invasion speed can be traced to the impact of kin competition. With low dispersal mortality ($\mu = 0.15$), the relative contribution to dispersal evolution drops to values at approximately 0.12. The reason is that, for high dispersal mortality, evolving emigration rates are usually low (Poethke et al. 2003; Bonte et al. 2012), which leads to a very pronounced local kin structure and thus a high kin-based benefit for emigration.

In our study, we concentrate on the effect of kin competition on the evolution of emigration rates during invasions. However, the example of the cane toad invasion in northern Australia is based on the investigation of the

mobility of individuals, which has increased during the invasion period (Phillips et al. 2008) and has enabled individuals to disperse over larger distances. Although the subject has been less intensively studied, it has been shown in theoretical studies that kin competition also has the potential to lead to wider dispersal distances (Rousset and Gandon 2002; Bonte et al. 2010; Starrfelt and Kokko 2010). Hence, we expect that results comparable to those presented here would have emerged if we had simulated the evolution of movement distance. As long as local kin structure is pronounced, enhanced dispersal will be especially favored during periods of range expansion. This may be attributable (nonexclusively) to either the evolution of higher readiness to leave the natal habitat or to selection for higher mobility resulting in a tendency to travel over longer distances.

Conclusions

With our results, we can show that kin competition is an important force driving dispersal evolution during inva-sions. However, its relative importance may depend on environmental conditions; under conditions that generally promote the emergence of pronounced local kin structure, such as small patches, low environmental stochasticity, and high patch isolation, kin competition may indeed be the dominant driver for the evolution of accelerating invasion speed.

Acknowledgments

APPENDIX

Unprocessed Simulation Results

Table A1: Values for invasion speed (ν) and marginal emigration rate (e) for different simulation scenarios

	Control scenario		Kin competition removed	
Parameter, value	ν	e	ν	e
K:				
150	.35, **.41**, .46	.33, **.47**, .68	.23, **.34**, .40	.06, **.35**, .48
50	.20, **.24**, .29	.21, **.35**, .50	.12, **.16**, .23	.06, **.10**, .33
λ:				
3	.45, **.54**, .62	.39, **.56**, .85	.27, **.35**, .55	.05, **.21**, .62
1.5	.15, **.18**, .21	.16, **.26**, .36	.10, **.13**, .15	.06, **.10**, .21
σ:				
.75	.30, **.36**, .41	.28, **.43**, .60	.22, **.26**, .34	.08, **.17**, .51
.25	.30, **.35**, .40	.30, **.42**, .55	.16, **.21**, .33	.03, **.10**, .36
μ:				
.45	.19, **.24**, .28	.21, **.29**, .42	.07, **.11**, .15	.01, **.04**, .16
.15	.41, **.48**, .60	.40, **.59**, .88	.39, **.45**, .50	.25, **.50**, .78
Standard	.30, **.35**, .39	.30, **.43**, .56	.18, **.23**, .33	.05, **.13**, .40

Note: Data are 0.05, 0.5, and 0.95 quantiles, respectively. Bold typeface indicates the 0.5 quantile (median value). Standard scenario means are as follows: $K = 100$, $\Lambda = 2$, $\mu = 0.3$, and '$\sigma = 0.5$.

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