

Notes and Comments

Changes in Community Size Affect the Outcome of Competition

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ABSTRACT: We examine the role of stochasticity and competitive ability in affecting competition between two species using models derived for population genetics. Just as changing population size affects the fixation of a new mutation, we show that changing the total number of competitors (i.e., community size) can alter the course of competitive exclusion across a wide range of initial starting densities of the two competing species. Shifts in competitive exclusion occur because changes in community size affect the relative importance of competitive ability and stochasticity in affecting the outcome of competition, potentially allowing inferior invaders to usurp superior residents. By shifting the role of stochasticity and competitive ability, any process that changes the total number of competitors in a habitat (e.g., disturbance, eutrophication, fragmentation, predation) may lead to shifts in competitive exclusion and the composition of communities.

Keywords: community composition, fragmentation, invasion, stochasticity.

Understanding the mechanisms determining the outcome of competition has tremendous value for understanding both basic (e.g., deciphering patterns of diversity; Hubbell 2001) and applied ecological problems (e.g., the invasion of exotic species; Seabloom et al. 2003). Although the outcome of competition has often been treated as deterministic (see review in Sommer and Worm 2002), stochasticity can have a substantial bearing on interactions among com-

petitors. For example, in Tilman's (2004) stochastic niche theory, stochastic mortality may remove propagules during the early stages of invasion, thereby altering the potential for invasion and coexistence. Stochastic shifts in the abundance of species generate widespread ecological patterns in the neutral theory described by Hubbell (2001). In the spirit of the neutral theory (Hubbell 2001), we describe another insight gleaned from population genetics that may have important implications for understanding the outcome of competition: changes in the total number of individuals in a community (i.e., community size; Hubbell 2001) alter the relative role of stochasticity versus competitive ability and thus alter the outcome of competition (fig. 1).

Competition between two species in a patch of habitat can be viewed as analogous to the dynamics between two alleles within a population. In this simple situation, one of two outcomes is eventually realized: either a new allele is lost from the population or it becomes incorporated ("fixed") across the entire population. New alleles (often new mutations) are more likely to fix when they are favored by natural selection, just as invaders are more likely to exclude resident species when they are superior competitors. However, stochastic forces can play an important role: even when beneficial, new alleles are often eliminated by chance, especially when they are rare in the population (Kimura 1962; Otto and Whitlock 1997). Building on previous work, Otto and Whitlock (1997) demonstrated that changes in population size can affect the relative importance of selection and stochasticity in determining whether a new allele will fix. When populations are growing, the role of stochastic forces in affecting fixation is reduced. Conversely, when populations are shrinking, stochastic forces play a more important role in determining fixation (Otto and Whitlock 1997).

Applying this concept from population genetics to the case of competitive exclusion can potentially provide novel insight into competitive interactions between species. Similar to the situation where an allele is in a growing or shrinking haploid population, we examine the likelihood of competitive exclusion in communities where commu-

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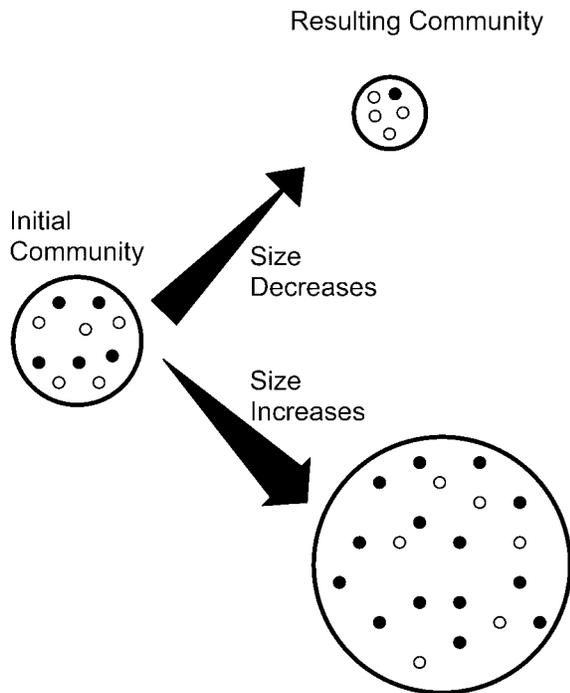


Figure 1: Conceptual figure of how changes in community size affect the outcome of competition. Each large circle represents a habitat capable of holding a finite number of two competing species. Half of the individuals in the reference community are superior competitors (*filled circles*), whereas half are inferior competitors (*open circles*). If the number of individuals in the community (i.e., the total population) is reduced in size, stochastic forces may eliminate the superior competitor despite its greater competitive ability, making it more likely that the smaller community will eventually come to be dominated by the inferior competitor. If the total population is increased, stochastic forces have less of an impact on the composition of the next generation, allowing the superior competitor to increase in frequency, increasing the likelihood that the superior competitor will eventually eliminate the inferior competitor from the patch of habitat.

nity size (i.e., the total number of organisms of two competing species) is either increasing or decreasing. Ecological processes that might lead to changes in community size include habitat degradation or nutrient enrichment (Vitousek et al. 1997), removal of a shared natural enemy (Sommer and Worm 2002), changes in habitat size or quality (Vitousek et al. 1997; Bender et al. 1998), or some other form of disturbance (Pickett and White 1985). The insight that emerges from this approach is that changing community size affects the outcome of competition.

Model Description

We examine the likelihood that a new species (an “invader,” as in Tilman 2004) either will eventually exclude

the resident species or will be defeated by the resident. We use the same methods developed by Kimura (1962) for calculating the likelihood that a new allele will fix in a population when stochasticity and selection are both present. Determining fixation probability requires knowledge of effective population size, N_e , the frequency of the new allele or invader, p , and s , which is the additive selective advantage of an allele in a diploid population and the relative selective advantage of an allele in a haploid population. In the context of interspecific competition, s represents the likelihood that an invader will survive to the next generation relative to the resident species. That is, the proportion of invaders in generation t will be equivalent to $(p_{t-1})(1+s)/C_{t-1}$, where $C_{t-1} = [1 - p_{t-1}(1)] + [p_{t-1}(1+s)]$, the average competitive ability of all the individuals in the habitat (analogous to the average fitness of a population). Thus, the proportion of invaders in the next generation is a function of their frequency weighted by their competitive ability relative to the competitive ability of the resident. Because competition is modeled in relative terms, the competitive ability of the resident is assumed to be 1 (hence $s = 0$ for the resident species). We model scenarios where invaders and residents are either weak competitors ($s = \pm 0.001$) or strong competitors ($s = \pm 0.01$).

Once these parameters are known, fixation probability, P , can be estimated using the formula of Kimura (1962), where we replace N_e with J_e (effective community size) to denote our application of the formula to competition:

$$P = \frac{1 - \exp(-4J_e sp)}{1 - \exp(-4J_e s)}. \quad (1)$$

Although fixation models generally examine the situation where a novel allele starts as a single copy (e.g., as in the case of a new mutation; Kimura 1962; Otto and Whitlock 1997), equation (1) can be used to calculate fixation probability across a range of starting frequencies (Kimura 1962). As such, equation (1) can be applied to realistic competition scenarios where competitors may encounter each other along a continuum of context-dependent frequencies, from rare introductions of invaders via long-distance dispersal events to situations where invaders exist at high frequencies within the community (e.g., because of close proximity of a propagule source; Sommer and Worm 2002).

Community change is modeled as logistic, where $J_{t+1} = J_t + rJ_t(1 - j_t/K)$; J_t represents community size at time t , r represents the intrinsic rate of population growth, and K represents carrying capacity. Effective community size is calculated using the formula of Otto and Whitlock (1997) for effective population size, whereby

$$J_e = \frac{J_i K(s+r)}{sK + rJ_i}. \quad (2)$$

For simplicity, competitor populations are assumed to have the same intrinsic rate of growth, $r = 0.1$, and the per capita contribution of competitors to J and K is equal (i.e., J is the sum of the number of both competitors, and competitors both compete within the same K). We model the haploid case of fixation because this is most readily interpretable in terms of competition. As such, J_e as generated with equation (2) is corrected to $J_e = J_e/2$ prior to use with equation (1) (Otto and Whitlock 1997). Using this approach, we investigate how relative competitive ability, changes in community size, and initial invader frequency influence the outcome of competition.

Model Results and Implications

When applied to competition, these models logically reveal that changes in the size of both competitor populations (community size) may affect the outcome of competition. When community size is increasing, superior invaders are more likely to become frequent enough to escape loss due to stochastic forces (fig. 1). When community size is shrinking, superior invaders are less likely to experience positive growth when rare, making them susceptible to loss due to stochastic forces (fig. 1). Although inferior invaders are always less likely to win in competition in absolute terms, they are relatively more likely to secure victory when community size is shrinking. This is because inferior invaders can never win by competing: they rely entirely on stochastic forces to achieve victory, and these forces are most important in populations that are small, declining in size, or both.

The greatest changes in fixation rates are expected to occur when the change in population size is large relative to s (Otto and Whitlock 1997). In terms of interspecific competition, this is illustrated by the effect of changing community size in large populations when competitors are weak (fig. 2B). In larger populations, changes in growth have a greater impact on weak competitors because total population size change is greater relative to small populations: small populations add 100 individuals in order to double, but large populations add 1,000 individuals to double (cf. fig. 2C, 2D). The rate of community size change, r , also affects the outcome of competition, with faster growth favoring victory of superior competitors and faster declines favoring the victory of inferior invaders (fig. 3). Otto and Whitlock (1997) have shown that fixation of alleles, and thus victory of competitors, is also affected when populations experience growth more dramatic than the logistic growth we depict. For example, exponential

changes in population size magnify the effect of growth or reduction on fixation relative to logistic growth. This can be seen analytically by using $J_e = J_i(1 + r/s)$ in conjunction with equation (1) (Otto and Whitlock 1997).

Even when community size is not changing, the importance of stochasticity may overwhelm competitive ability in small populations. For example, new alleles in diploid organisms are considered effectively neutral when $4N_e s < 0.1$ (Kimura 1964). The increasing effect of stochasticity when community size is small is why weak competitors in small populations are basically neutral (fig. 2A), where the probability of victory is close to the initial frequency of the species in the community (i.e., a slope of 1; fig. 2A), regardless of changes in community size. This is because small community size (small J_e ; Hubbell 2001) and small differences in competitive ability (small s ; fig. 2) both increase the role of stochasticity in affecting the outcome of competition.

Movement may link competitors in space, leading to metacommunity dynamics where inferior competitors persist regionally via colonization of patches where superior competitors are not found (Sommer and Worm 2002). This work suggests that poor competitors may not need to rely on superior colonization ability to find patches that are completely devoid of competitors (i.e., the competition-colonization trade-off; Sommer and Worm 2002). Rather, poor competitors may only need to find patches where community size is low enough, or shrinking in size fast enough, that competition with superior residents is of relatively less importance because stochasticity governs victory. In general, the degree to which communities are linked via movement of individuals will also affect the relative role of stochasticity and competitive ability in influencing victory, because connectivity is one determinant of the overall size of the community. Stochasticity is expected to be more important in more fragmented, disjunct communities than in a community of the same overall size that is more connected, leading to increased “community drift” among more disjunct communities (Hubbell 2001).

Ultimately, many generations are required for true competitive exclusion (or fixation of an allele), and thus many ecological systems may exist in a dynamic equilibrium whereby complete competitive exclusion is rarely realized. Recurrent changes in community size may contribute to such long-term temporal persistence because fluctuations in the overall size of competitor populations would lead to temporal shifts in the relative importance of stochasticity and competitive ability. This is illustrated by estimators of fixation probability in fluctuating populations (reviewed in Otto and Whitlock 1997), where N_e in cyclic populations is calculated as the harmonic, not arithmetic, mean of population size. As such, inferior invaders that would rapidly be eliminated from large, stable commu-

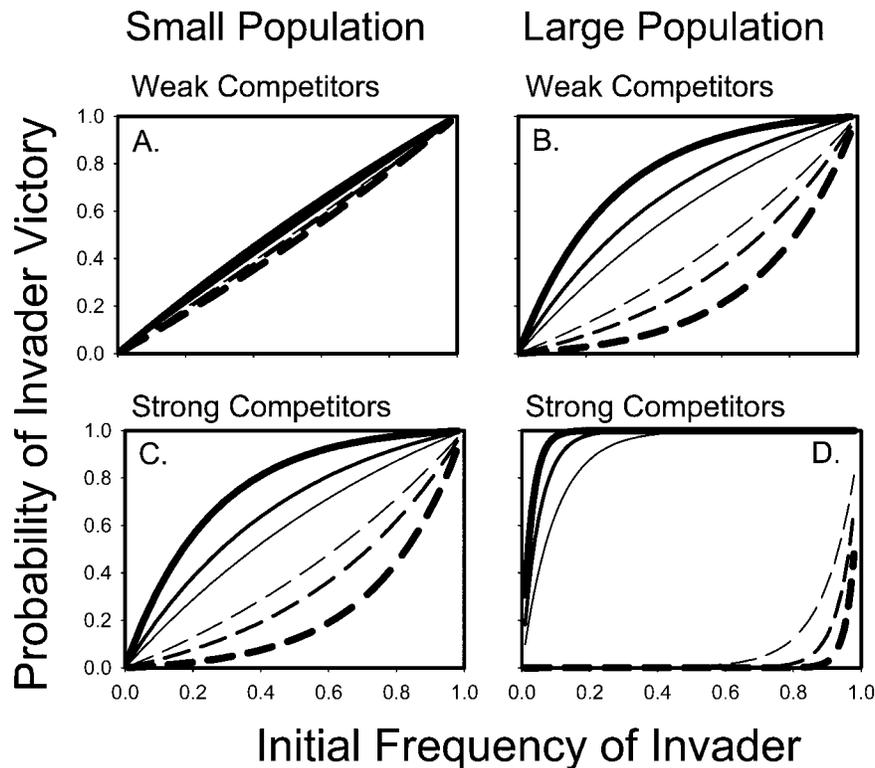


Figure 2: Changes in the likelihood that an invader will eventually exclude a resident competitor in communities that undergo a change in community size (J). Small communities start with 100 total individuals (A, C; $J_0 = 100$), whereas large communities start with 1,000 (B, D; $J_0 = 1,000$). Changes in community size are produced by altering K (the number of both competing species a habitat can support) so that communities either grow, becoming twice as large as the starting community (*thick lines*; $J_{\text{final}} = K = 2J_0$), remain the same (*medium lines*; $J_{\text{final}} = K = J_0$), or are reduced to half the starting size (*thin lines*; $J_{\text{final}} = K = J_0/2$). Solid lines represent the case where invaders are superior competitors that are either weak competitors ($s = 0.001$; A, B) or strong competitors ($s = 0.01$; C, D) relative to the resident species. Dashed lines represent the case where invaders are either weakly ($s = -0.001$; A, B) or strongly ($s = -0.01$; C, D) inferior to residents. Growth is modeled as logistic with $r = 0.1$. For reference, if competitors are completely neutral ($s = 0$), with no difference in competitive ability, the probability of invader victory is equivalent to initial frequency of the invader (i.e., slope of 1).

nities might persist for considerable amounts of time in unstable communities where community size fluctuates. Even if the arithmetic mean size of both communities is the same, the effective size of the community (J_e) would be lower in the fluctuating community, reducing the role of competitive ability in eliminating inferior competitors (to obtain this result analytically, use the harmonic mean in conjunction with eq. [1]). The potential for such “bottlenecks” to shift ecological communities has been demonstrated by Vellend (2004): forest floor herb communities in secondary forests that had been dramatically reduced in size exhibited greater divergence in species’ relative abundance compared with communities in primary forests where community size has been more stable in time. Similarly, the increased role of stochasticity when J_e is reduced may contribute to empirical findings that communities that are frequently disturbed are more susceptible to in-

vasion (e.g., Thompson et al. 2001) and that disturbance promotes the dominance of exotic plants that are competitively inferior to residents (Seabloom et al. 2003).

The key insight from our model, gleaned from population genetics, is that changing community size shifts the role of stochasticity versus competitive ability in determining the outcome of competition. Although the model we present makes several implicit assumptions (e.g., habitats are homogeneous in the distribution of their resources, and competition is waged through differential survival rather than direct competition for resources), the simplicity of the underlying dynamics suggests that its conclusions and utility are likely to extend to neutral models (Hubbell 2001), non-neutral models that also include stochasticity in initial rates of propagule establishment (Tilman 2004), or any other model of competition where stochastic forces are allowed to operate. This generality is reinforced by simulations using

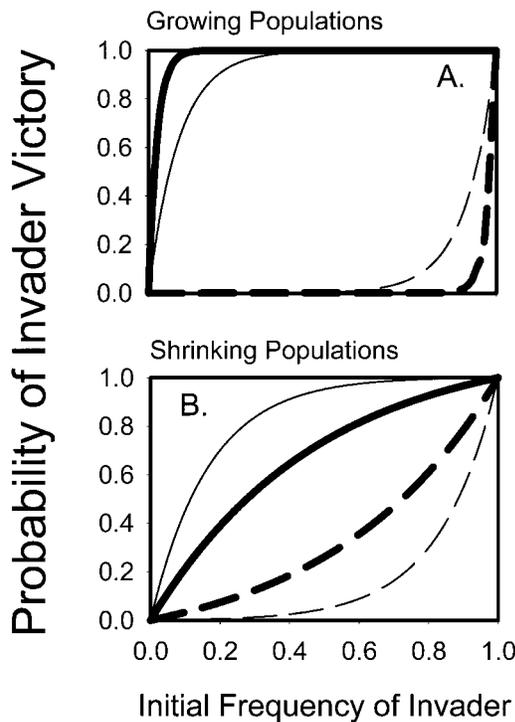


Figure 3: Rate at which community size changes affect the likelihood of eventual competitive exclusion. For both panels, community size begins at 1,000 individuals ($J_0 = 1,000$), then either increases to 5,000 individuals (A; $J_{\text{final}} = K = 5J_0$) or declines to 200 individuals (B; $J_{\text{final}} = K = J_0/5$). Changes in community size are modeled using the logistic model, with thick lines representing the outcome when the rate of community size change is large ($r = 0.1$) and thin lines representing the outcome when the rate of community size change is reduced ($r = 0.001$). Solid lines represent the situation where invaders are superior competitors relative to residents ($s = 0.005$); dashed lines represent the outcome when invaders are inferior competitors ($s = -0.005$).

standard Lotka-Volterra competition models, which produce the same results as our model based on population genetics (appendix in the online edition of the *American Naturalist*). Moreover, these models demonstrate that the results from our model also apply to cases where competitors differ in K and r (appendix).

This work suggests that the outcome of competitive interactions may be directly influenced by changes in habitat size or habitat quality, because these factors ultimately determine the number of organisms a habitat can support (i.e., the total number of invaders and residents). Anthropogenic activities affect habitat quality via fragmentation, pollution, changes in nutrient flow, and outright destruction (e.g., Vitousek et al. 1997; Bender et al. 1998). Given the scope and severity common to anthropogenic habitat alteration (Vitousek et al. 1997), it may have particularly influential impacts on competitive exclusion because changes

in community size are likely to be large (e.g., fig. 2), and the rate at which the change is realized is likely to be rapid (fig. 3). Succession and natural disturbance (Pickett and White 1985) also lead to changes in habitat quality that affect the number of organisms a patch can support. As such, understanding processes that affect community size may be directly relevant for understanding the persistence of diverse communities in time and space and for providing insight into how anthropogenic habitat modification may affect the victory of inferior competitors.

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