DISSERTATION

ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF ALLEE EFFECTS IN SMALL FOUNDER POPULATIONS OF INVASIVE SPECIES

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ABSTRACT

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Despite the obvious threats invasive species pose to ecosystem health, studying the characteristics that influence their colonization can provide valuable insight on fundamental issues in ecology, evolution, and biogeography. The aim of this research has been focused on the implications of mechanisms likely to affect persistence of small founder populations. Individuals can suffer a reduction in one or more components of fitness when population growth and spread are constrained at low density. This dynamical relationship between fitness and population size (i.e., positive density dependence) can be driven by a myriad of mechanisms, broadly termed Allee effects. In this dissertation, I have theoretically explored how small founder populations faced with Allee effects can overcome the demographic challenges that heighten the risk of extinction. I have developed models of increasing complexity to better understand the ecological and evolutionary consequences of Allee effects.

I begin by exploring ways in which intraspecific interactions influence population dynamics and invasiveness through a review of the literature. The mechanisms that impact individual fitness at low density suggest that there are benefits to being in a large population; however, there are abundant examples of adaptations that might have evolved in small or sparse populations in response to Allee effects.

Using a reaction-diffusion framework with a quantitative genetics approach, I have derived conditions and explored the dynamics for rapid adaptive evolution rescuing the population from extinction. This deterministic modeling approach broadly describes population dynamics through diffusive dispersal and density dependent growth, where the response to population density can evolve through a genetic subsystem that incorporates the intensity of selection and genetic variance. For both the spatial and non-spatial cases, invasion criteria were determined across the range of parameter space. The results emphasized that a sufficient amount of genetic variance is a crucial component for evolutionary rescue to occur.

I developed a spatially explicit, individual-based stochastic simulation in order to more realistically capture the complexity of intraspecific interactions. I found that with limited dispersal and local perception, the emergence of spatial structure impacted individual fitness and could enable population persistence. Departures from the population-level model predictions demonstrate the importance of considering individual variation in assessing the consequences of Allee effects.

I further incorporated immigration and genetic variation into the simulation in order to explore the relative importance of evolutionary, demographic, and genetic rescue for establishment. Additional immigration was more effective than adaptive evolution in contributing to successful invasions due to the intensity of ecological constraints on population growth and time to extinction. Without multiple introductions, evolutionary processes can contribute to recovery through genetic variation maintained and enhanced by mutation and recombination. Overall, I have demonstrated that it is possible for a

small founder population to overcome a suite of ecological, evolutionary, and genetic obstacles upon introduction into a novel environment despite the paradox of invasion.

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CHAPTER 1

Why intraspecific interactions matter in invasion biology

Introduction

Organisms that are released into areas outside of their native ranges often face many novel challenges in the struggle for survival and reproduction. Small founder populations are especially at a disadvantage due to the elevated impact of stochastic variation and other environmental and demographic constraints limiting establishment success. Despite these difficulties, invasive species represent the second greatest threat (after habitat loss) to global biodiversity (Williamson 1996) and cost the United States alone over $100 billion annually (Pimentel et al. 2000). The paradox of biological invasion, broadly considered the ability to overcome limitations and successfully invade (Sax and Brown 2000; Hufbauer 2008), has garnered significant attention in the last decade (Lockwood et al 2007; Davis 2009) and is based on extensive foundational literature (e.g., Elton 1958; Baker 1965; Ebenhard 1988; Drake et al. 1989; Hengeveld 1989; Williamson 1996). Whereas much of the seminal body of work implicitly addresses characteristics of invading species that make them good colonists, recent studies have proposed an integrative framework that combines ecological and evolutionary hypotheses to explain invader success following introduction (Hufbauer and Torchin 2007, and references therein). To further conceptualize invasion theory, Shea and Chesson (2002) point to three main factors that contribute to an invader's growth rate: resources, natural enemies, and the physical environment. Hence, the ability to

respond to these factors will determine the overall success and invasiveness of a population (Shea and Chesson 2002). I propose that in addition to these inherently important factors, changes in the endogenous environment (i.e., dramatic fluctuations in population size and structure in the introduced range) can significantly impact intraspecific interactions that may be critical to the success of an invader. Understanding how this novel selection pressure arising from density dependent reproductive and survival rates affects the fate of individuals and the founder population coupled with the characteristics (e.g., life-history traits, aggregation formation) to overcome these limitations is a necessary component of an integrative framework of the factors promoting invasion.

The classical view of intraspecific interaction and density dependence on population dynamics is generally focused on competition and regulation through the negative effects of over-crowding (e.g., Nicholson and Bailey 1935). Although populations at low density are relieved of those constraints, many species rely on cooperative or gregarious behaviors when foraging, evading natural enemies, raising their young, conditioning their environment, or locating and selecting mates (Courchamp et al. 2008; Tobin et al. 2011). These positive density dependent relationships are often referred to in the literature as Allee effects (originally coined, 'the Allee principle,' by Odum, 1953) after the Chicago ecologist who first identified the phenomenon (Allee 1931, 1938; Allee et al. 1949). Even though the dynamical consequences of Allee effects can vary in space and time due to community interactions or environmental factors (Tobin et al. 2007), the mechanisms behind Allee effects are fundamentally mediated by population density. The formal definition proposed by Stephens et al. (1999) emphasizes

the distinction between a decrease in one or more fitness components of an individual from a decrease in population density (i.e., component Allee effects) and an overall decline in per-capita population growth rates in a low-density population (i.e., demographic Allee effects). In general, it is useful to distinguish between component Allee effects and demographic Allee effects in order to recognize whether density dependent effects on components of individual fitness scale up to impact population growth. Since component Allee effects may not always generate demographic Allee effects (i.e., a reduction in overall individual fitness is compensated by other fitness components that may benefit from low density; Courchamp et al. 2008), populations can experience demographic Allee effects ranging from 'weak' to 'strong' (Wang and Kot 2001; Deredec and Courchamp 2003). 'Strong' Allee effects produce negative per-capita growth rates when the population density falls below a critical threshold, whereas populations with 'weak' Allee effects have no lower threshold to exceed, but experience reduced per-capita growth rates at low densities (Taylor and Hastings 2005). Making the distinction between weak and strong demographic Allee effects is useful for managers and modelers using census data from the population-level perspective in order to identify trends in per-capita growth rates and population dynamics.

In one form or another, it is likely that most failed introductions succumb to Allee effects in addition to stochastic mortality because non-native species often arrive in such low numbers due to the difficulty of surviving extreme conditions during transport (Williamson and Fitter 1996; Liebhold and Bascompte 2003; Simberloff and Gibbons 2004; Lockwood et al. 2005; Drake and Lodge 2006). Based on this observation, it is clear that increased propagule pressure (i.e., introduction effort that is a composite

measure of size and number of release events; Lockwood et al. 2005) can significantly reduce the risk of extinction (Stiling 1990; Hopper and Roush 1993; Leung et al 2004; Lockwood et al. 2007; Simberloff 2009). Although little known about failed invasions, it is not always clear why some invasions, especially those starting from small founder populations, succeed (Lockwood et al 2007). With increased management protocols regulating introductions, evidence of populations establishing from low numbers, and invader dynamics that are best explained by Allee effects (e.g., long lag times and slower spread; Taylor and Hastings 2005), it seems a "reversal of fortune" (Elam et al. 2007) likely occurs wherein individuals within small populations overcome their limitations and reproduce and spread successfully.

In this review, I focus on two ecological attributes of small populations of invasive species that give rise to component Allee effects and influence risk of extinction: mating systems and dispersal modes. Not only are these attributes easily studied in invasive species, these characteristics strongly impact population growth and are two main factors that contribute to positive density dependence when fitness is primarily affected by the endogenous environment and intraspecific interactions. In the following sections I highlight empirical and theoretical studies that have examined these ecological attributes in order to demonstrate the importance of intraspecific interactions in the success of invasive species. Additionally, I discuss the ecological and evolutionary consequences of reduced intraspecific interaction and the emergence of adaptations that may have arisen to mitigate the mechanisms behind Allee effects, in order to provide a general context to help reconcile the paradox of invasion with the added complexity of positive density dependence.

Mating systems and mate-finding Allee effects

One of the most intuitive and widely cited mechanisms for generating a component Allee effect is mate-finding (Stephens et al. 1999; Gascoigne et al. 2009; Yamanaka and Liebhold 2009). Baker's Law (Baker 1955) suggests that in demographic situations where the reproduction of individuals is limited by an absence of pollinators, gametes, or mates, establishment is much more likely for organisms with uniparental reproductive systems due to fecundity assurance (Eckert et al. 2006). Whereas some invasive species have evolved selfing from outcrossing (e.g., Brazilian water hyacinth, *Eichhornia paniculata* (Barrett et al. 2008) and the parthenogenetic crayfish, Marmorkrebs, *Procambarus fallax* f. *virginalis* (Feria and Faulkes 2011)), self-incompatibility and sexual reproduction are nonetheless not rare for invasive species. When outcrossing organisms are faced with low population density, however, reproductive fitness can be affected significantly by the inability to find a mate or meet gametes (in the passive process of external fertilization and plant pollination), or moderately, with a reduction in reproductive potential through lack of multiple matings and/or poor mate quality (Gascoigne et al. 2009). Although it is difficult to detect demographic Allee effects (i.e., the cumulative effect on per-capita fitness) due to varying strengths of component Allee effects, there are a number of empirical studies that have identified how small population size affects reproductive success and survival in invasive species. First, I will focus on evidence from mate-finding Allee effects and fertilization success for sessile, dioecious organisms through dispersal of gametes, and then discuss active searching for and attracting mates.

Dispersal of gametes

As a model system in invasion biology (identified as such by Parker 2004), a well documented example of pollen limitation is the wind-pollinated smooth cordgrass (*Spartina alterniflora*), which shows an 8-fold disadvantage in seed production at low density (Davis et al. 2004). Another wind-pollinated invader, common ragweed (*Ambrosia artemisiifolia*), possesses several traits that offset Allee effects, such as the production of large quantities of windborne pollen, prolific seed production, and dormant seed banks (Barrett 2010). Elam et al. (2007) found that in the self-incompatible California wild radish (*Raphanus sativus*), maternal fitness not only declines with population size but also with genetic relatedness from incompatible genotypes. They suggest, however, that seeds from as few as three or four fruits set by different plants in addition to the apparent adaptation of half-sibling, multi-seeded fruits can result in minimal Allee effects. Although there does not seem to be pollinator limitation in the California wild radish or other buzz-pollinated plants (e.g., *Senna didymobotrya*, van Kleunen and Johnson 2005), fertilization probability can be further reduced not only by the presence of few conspecifics, but also the abundance of pollinators (e.g., Scotch broom (*Cytisus scoparius*), Parker 1997). Some modeling studies have shown that depending on the strength of inbreeding depression, the strength of pollen-limitation Allee effect, fertility and the initial state of partial selfing, natural selection can result in plants evolving either complete selfing or complete non-selfing (Cheptou 2004; Morgan et al. 2005). It seems, however, that both of these extremes can lead to population extinction through 'evolutionary suicide,' and that different model assumptions should yield intermediate selfing rates with a trade-off between maximal fertilization and inbreeding avoidance (Gascoigne et al. 2009).

Although plants are an obvious example of how fertilization efficiency can be positively related to population density through pollen limitation, some animals disperse gametes externally and are also either sessile or reproduce without direct contact with conspecifics (e.g., many marine invertebrates). Broadcast spawners have similar limitations to outcrossing plants, whereby they rely on the meeting of gametes externally. A well-documented case of an aquatic invader that sheds gametes into the water is the zebra mussel (*Dreissena polymorpha*; Johnson and Carlton 1996). Although zebra mussels possess traits that make them exceptional invaders (e.g., they can exploit food resources through active filter feeding and can easily take advantage of human-mediated dispersal mechanisms, Johnson and Carlton 1996), dilution of gametes when individuals are spaced far apart will decrease fertilization rates (Denny and Shibata 1989; Leung et al. 2004). Synchronous spawning observed in zebra mussels (Haag and Garton 1992) may mitigate dilution effects; however, founding populations of sessile adults must be either large or quite spatially aggregated (Johnson and Carlton 1996). Although his study species is not invasive, Levitan (2002) developed a nice comparison of three congeneric sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus*, and *S. droebachiensis*) that demonstrates how sperm limitation may stimulate the evolution of gamete morphology and performance.

Based on these examples thus far, it is clear that mate-finding component Allee effects can negatively affect reproductive success, especially when mature individuals cannot move, however the connection from component Allee effects to demographic Allee effects is not always clear. As much of the empirical evidence comes from successful invaders, it is difficult to determine the strength of demographic Allee effects

due to mitigation of component Allee effects through adaptations, fitness tradeoffs, and spatial structure in populations. In the passive dispersal of gametes, I have discussed some adaptations that may have arisen to increase fertilization efficiency. Additionally, even in the presence of a positive relationship between reproductive output and density, other fitness components may be negatively density dependent and balance the cost-to-benefit ratio of overall fitness. Lastly, when individuals are spatially aggregated, although the global density may be low, the local density that individuals experience may be sufficient to overcome mate-finding component Allee effects. Along these lines, dispersal contributes to reducing isolation and increasing connectivity between individuals, sub-populations, or populations. In the following section on active movement and mate-finding, the wide range of animal behavior and dispersal can fluctuate component Allee effects in time and space and provide different opportunities for increased fitness.

Searching for and attracting mates

Although active movement behavior increases the complexity of many animal mating systems (Morrell and James 2008), mate-finding component Allee effects nonetheless exist at reduced density. Because individuals will not always be able to find a suitable, receptive mate during their own receptive period, this positive density dependent relationship can impact reproductive output. The Chinese mitten crab (*Eriocheir sinensis*), for example, which after migrating from freshwater streams to the brackish waters of estuaries, must find a mate by physical contact, as opposed to release of a pheromone into the water to attract mates (Herborg et al. 2006). Despite this strong Allee effect and their semelparous life history, high fecundity of just one fertilized female

can lead to population persistence (Jerde et al. 2009). Another harmful aquatic invader, the spiny water flea (*Bythotrephes longimanus*), is a cyclic parthenogen, a strategy that should reduce the magnitude of an Allee effect. Because sexual reproduction is a required part of the life cycle, even at densities that were orders of magnitude higher than the theoretical critical threshold density, Gertzen et al. (2011) found that the probability of mating declined and substantially lowered establishment success. The authors suggest that mate finding was affected by swimming speed, detection distance and the duration of the mating phase. They argue that since water fleas have some capacity for sex-determination, organisms should modify their sex ratios to reduce Allee effects (Gertzen et al. 2011). Where Kramer et al. (2008) demonstrate that below a critical density, mate encounter rate limits the colonization success of a diaptomid copepod (*Hesperodiaptomus shoshone*; but see Yen et al. 2011 showing that males detect female pheromones), Becheikh et al. (1998) report that a parasitic copepod (*Pachypygus gibber*) can overcome mate limitation by sexual differentiation of larvae, depending on availability of sexual partners. Hopper and Roush (1993) found that introductions of small populations of parasitoids for biological control often fail because females are unable to find mates and unfertilized eggs develop into haploid males (arrhenotoky), resulting in too few females to maintain a viable population.

Other invaders with apparent adaptations to overcome mate limitation and reduce the strength of Allee effects include, apple snails (*Pomacea canaliculata*) with chemotactic detection mechanisms and females that store sperm (Jerde et al. 2009), flour beetle (*Tribolium confusum*; Allee 1941) males use a pheromone to attract both sexes while females produce a different pheromone to attract just males (O'Ceallachain and

Ryan 1977), the Cuban tree frog's (*Osteopilus septentrionalis*) male vocal advertisements and the absence of high mating selectivity by females (Salinas 2006), and the red deer (*Cervus elaphus*) where induced ovulation occurs (Jabbour et al. 1994).

Using a large data set from 150,000 pheromone-baited traps that spanned a geographical range from North Carolina to northeastern Minnesota, Tobin et al. (2007) investigated threshold dynamics and speed of the gypsy moth (*Lymantria dispar* L.) invasion. They found demographic Allee thresholds associated with smaller populations due to failure to find mates – further Johnson et al. (2006) showed that those thresholds varied across space and time affecting the speed of invasion (Johnson et al. 2006). Although the variation in Allee effects could be due to differing predation pressure across regions (Tcheslavskaia et al. 2002), there is speculation that it may be that the effectiveness of pheromone transmission for mate-finding in gypsy moths varies with environment (Gascoigne et al. 2009) or with individuals. In a modeling study, Jonsson et al. (2003) found that for pheromone versus non-pheromone mate-finding strategies represented by two families of saproxylic beetles (Anobiidae (genus *Dorcatoma*) and Cisidae, respectively), the pheromone strategy was relatively more efficient when the relative density of insects or the density of host trees decreased. In an obligatory mutualism for their survival and reproduction, the devastating pinewood nematode (*Bursaphelenchus xylophilus*) relies on the invasive pine sawyer beetle (*Monochamus alternatus*) as its vector for transmission to host pine trees (genus *Pinus*) to infect while making it suitable for oviposition by the beetle (Togashi and Shigesada 2006). This circumstance leads to an Allee effect in that the basic reproductive rate depends on the availability of minimum densities of both vector and host, with disease persistence more

sensitive to the density of pine sawyer beetles (Yoshimura et al. 1999). An Allee effect also emerges in the beetle dynamics, where they need to contact the pine tree at least twice to reproduce successfully (first to introduce the nematode and then after an incubation period when the tree is ready for oviposition; Takasu 2009). The interesting point that Takasu (2009) makes is that beetle mobility in addition to the incubation period influence dynamics, and that localized beetle dispersal can hinder the emergence of the Allee effect.

Similar spatial effects influence the spread of a microbial infection in fruit flies (*Wolbachia*, Turelli and Hoffman 1991) and the karnal bunt wheat pathogen (*Tilletia indica*, Garrett and Bowden 2002). The mutualistic relationship is also mirrored in schistosomiasis, where infection from the schistosome (i.e., digenetic nematode) in humans is dependent on population sizes of primary (i.e., humans) and secondary (i.e., an aquatic snail) hosts (Anderson and May 1991; Yoshimura et al. 1999). Disease prevalence (i.e., mean parasite burden per host) also exhibits an Allee effect because nematode sexual reproduction is decreased with scarcity of mating opportunities, but does not suffer when the nematode distribution is aggregated within the human host (Anderson and May 1991). This notion of quorum sensing is seen in pathogenic microbes (such as *Staphylococcus aureus*) where a minimum population density is often required to initiate expression of virulence factors needed to establish successful infections (Kadam and Velicer 2006). Additionally, there are obvious ties with Allee effects and abundance thresholds when disease dynamics interact with both host and pathogen/parasite densities and spatial structure (e.g., Anderson and May 1991; Regoes et

al. 2000; Boots et al. 2004; Deredec and Courchamp 2003; Lloyd-Simth et al. 2005; Davis et al. 2008; Hilker et al. 2009).

As is evident in all of these examples of reproductive systems and mate-finding Allee effects, population growth and individual fitness are inherently mediated through the interaction of individuals. Therefore dispersal modes and spatial context will necessarily drive invasion dynamics.

Dispersal modes and spatial consequences of Allee effects

In the following section, I will demonstrate how dispersal interacts with component Allee effects in general and the consequences for population establishment and spread. In the model that Veit and Lewis (1996) constructed to predict the rate of spread of the invasive house finch (*Carpodacus mexicanus*), they found that they could closely match the empirically observed pattern (i.e., accelerated spread following an initial period of slower growth) by incorporating a mate-finding Allee effect. From the empirical data, they ascertained that house finches disperse individually rather than in flocks, which demonstrates that at least along the outer fringes of the population, breeding success is reduced because birds could not find mates (Veit and Lewis 1996). Hence, the process of new species establishment is not only important following initial arrival, but it is also linked to the rate of spread.

As demonstrated throughout this dissertation, there is an important feedback relationship between dispersal and population growth. This idea links to some of the first work involving spatially explicit ecological modeling. For example, to address patchy distributions of plankton, Skellam (1951) recognized a tradeoff, where the size of the water mass (beyond which plankton cannot survive) is critical to counterbalance local

reproduction within the patch and the loss due diffusion on the boundary, to sustain a population (Kierstead and Slobodkin 1953). The effect essentially comes from the ratio of surface area to volume of a sphere being inversely proportional to its radius (Okubo 1980). So in a larger aggregation relatively fewer individuals are on the periphery than in a smaller one, and if it exceeds a minimum critical size, a plankton bloom occurs. This conceptual framework is broadly applicable, whether considering exogenous factors on growth and spread and/or the endogenous environment (i.e., population density, as is done throughout this dissertation). Thus, a general spatial consequence of Allee effects is the existence of a critical threshold in the area the population needs to occupy in order to persist. This spatial threshold is a function of initial population density, strength of the Allee effect, and the rate and distance of dispersal (and grows with number of spatial dimensions; Taylor and Hastings 2005). Lewis and Kareiva (1993) formally present this with an analytical calculation for a partial differential equation (PDE) model incorporating Allee effects (used throughout this dissertation); and Drake et al. (2005) have applied it for estimating volumes of untreated ballast water discharge for the probability of establishment of sexually reproducing, planktonic taxonomic groups including ctenophores, cnidaria, arthropods, annelids, as well as mollusks, echinoderms, and fishes. Vercken et al. (2011) were the first to empirically document evidence of a critical spatial Allee effect. They found that the probability of persistence of gypsy moth populations from one year to the next was positively associated with population area and dependent on initial population density (Vercken et al. 2011). This prediction has also been shown to be a general property of Allee effects in spatial models including other

PDE models (Soboleva et al. 2003), integrodifference equation models (Kot et al. 1996), and individual-based simulations (Etienne et al. 2002).

Along with the constraints on the size of the area that a founder population needs to occupy to overcome Allee effects, this approach has also informed observed patterns of colonization (Soboleva et al. 2003; Davis et al. 2004) and spread rates (Lewis and Karieva 1993; Shigesada and Kawasaki 1997; Keitt et al. 2001; Johnson et al. 2006; Tobin et al. 2007). Like what was observed in the house finch, Allee dynamics result in initial transient periods within which populations do not expand, slower rates of spread, and invasion pinning (Keitt et al. 2001; Taylor et al. 2004; Tobin et al. 2007). Since a change in total population size is determined by a race between reproduction in the population core (where the local density exceeds the Allee threshold) and dispersal at the periphery (where individuals do not contribute to growth because they are below the Allee threshold), the spatial spread at the invasion front is being pushed from the inside out as opposed to being pulled by the leading edge (Lewis and Kareiva 1993). Note, however, that in addition to demographic constraints, patterns of spread can be affected by the type of landscape being considered. While assuming there is no change in the underlying habitat quality or other exogenous factors, contiguous patches (i.e., discretization of the habitat) can stop spread at an edge because individuals, partly limited by local carrying capacity, cannot spill-over fast enough to the next patch to get above the threshold for population growth (Keitt et al. 2001); whereas continuous-space models (used in this dissertation) do not have these boundary effects. Based on these spatial dynamics, it follows that the presence of Allee effects are often invoked to explain the lag time before newly established populations spread and increase to a noticeable abundance

(Simberloff 2009). As such, empirical evidence is limited to well-studied species (e.g., the house finch, Veit and Lewis 1996; zebra mussels, Johnson et al 2006; gypsy moths, Liebhold and Tobin 2006; smooth cordgrass, Davis et al 2004).

To begin considering spread, it is important to remember that the population needs to overcome Allee effects and establish in the first place. This can happen as a result of increased propagule pressure or through particular traits that enable an organism to cope with low density. For instance, many of the strategies mentioned above to facilitate reproduction and mate-finding in a spatial context, in addition to general dispersal strategies including short distance spread (e.g., rhizomatous growth), post-reproduction dispersal, increased gamete or pollen production, and limited and lower propensity for dispersal. Fowler (2009) examined the possibility of density dependent dispersal, however from a somewhat counter-intuitive perspective. Where other density dependent dispersal models with Allee effects have addressed dispersal probabilities that increase with increasing density (e.g., Amarasekare 1998; Etienne et al. 2002; Stephens et al. 2002; Greene 2003), Fowler's (2009) approach suggests that decisions for dispersal could be based on leaving patches within which individuals experience reduced fitness (e.g., from low density, inbreeding) to search for sufficient density of conspecifics to increase reproductive output. Not surprisingly, Fowler (2009) found that local population dynamics remained qualitatively unchanged until the unstable population (with sufficiently high fitness threshold) was eventually driven to global extinction. If, however, a time limit for sampling is imposed between generations (i.e., restricted number of dispersal attempts), and based on the number of patches in the environment, the population could stabilize and be rescued from global extinction (Fowler 2009).

Rather than individuals trying to optimize their fitness based on limited information, Travis and Dytham (2002) observe that when incorporating Allee effects into their model exploring the evolution of dispersal during invasions, there was less intense selection for high dispersal propensity toward the invasion front than when Allee effects are ignored, and resulted in slower range expansion. And other research has shown that spatially structured populations with an Allee effect may suffer from evolutionary suicide with increased dispersal (Gyllenberg et al. 2002; Rousset and Ronce 2004; Parvinen 2007).

The ways in which component Allee effects influence individual behavior and population dynamics through positive density dependence can have interesting long-term implications. Some of the mechanisms invoked as means to surmount the obstacles associated with low population density can reduce overall population spread or give rise to genetic inbreeding as a consequence of spatial aggregations, however these future tradeoffs would not even be considered if the small population does not establish and survive in the first place. Additionally, many long-term consequences linked to overcoming Allee effects have not directly been empirically observed. Just as the connection between component Allee effects and demographic Allee effects is not always obvious, the demographic consequences of the emergence of different strategies will require further investigation.

Conclusion

Although it is clear from this review that overcoming dependencies on intraspecific interactions can help small populations succeed, there are nonetheless significant fitness advantages that result from the formation and continuation of animal aggregations as originally posited by Allee (1931). Thus, to fully understand traits that

mitigate Allee effects and allow small founder populations to establish and become invasive, it is essential to recognize fitness trade-offs and future costs when the population reaches higher densities. In the short-term, these trade-offs could mean reallocating resources from growth to reproduction (or vice versa). Long-term consequences could include: lower quality offspring if selectivity for a mate is reduced (e.g., the Cuban tree frog), decreased fitness of parent or offspring with increased reproductive output (e.g., reduced parental care, Andersson 1994; plants with high seed set suffered reduced growth and reproduction the following year, Ehrlen and Eriksson 1995), more reproduction and limited dispersal can increase intraspecific competition for resources, and genetic costs, such as inbreeding due to local mating and asexual reproduction and hybridization with other species when the adaptation for increased sperm production continues at high density (Levitan 2002). In addition to these trade-offs, Berec et al. (2007) highlight examples of interacting multiple component Allee effects, suggesting that reducing the negative impact of one component Allee effect may not have any effect on overall fitness.

To better understand the process of invasion, a full understanding of the behavior of populations at low densities is imperative. There are many extensive reviews on the characteristics of good invaders (Drake et al. 1989; Kolar and Lodge 2001; Sakai et al. 2001; Lockwood et al. 2007; Davis 2009), although only recently have invasion biologists begun to realize the role of Allee effects. Understanding Allee effects (and threshold dynamics) and the importance of intraspecific interactions for many species has been used extensively in conservation efforts (Stephens and Sutherland 1999) and managing infectious diseases (Anderson and May 1991). It is now evident that Allee

effects influence the dynamics of invasive species (Taylor and Hastings 2005), and can be used to help inform predictive hypotheses and risk assessments for establishment and spread. From this perspective, Tobin et al. (2011) highlight current strategies to effectively exploit Allee effects, and propose novel means to control biological invaders. Overall, the general perspective is that eradication strategies need to cull a population only to a level below their Allee threshold while focusing on the primary mechanisms that contribute to component Allee effects (Liebhold and Bascompte 2003; Tobin et al. 2011). Along with identifying the component Allee effects, managers should be aware of how the population arrived and established in the first place to reveal underlying traits and adaptations that enhanced persistence, in addition to whether those mechanisms sustain the population at low density (essentially reducing the Allee threshold; e.g., detection of scarce conspecifics) or function to increase the density (without impacting the Allee threshold; e.g., high fecundity).

Lastly, it is obvious that populations do not operate in isolation and there are countless exogenous factors that influence population dynamics (e.g., habitat quality, climate, interspecific interactions). But since "the supreme goal of all theory is to make the irreducible basic elements as simple and as few as possible without having to surrender the adequate representation of a single datum experience" (Einstein 1934), I focused this review and this dissertation on endogenous selection pressure and intraspecific interactions in a small founder population. There are many other invasive species that do not exhibit Allee effects and far more species in their native ranges with low population sizes that are unable to overcome Allee effects and are therefore endangered (Soule and Wilcox 1980). Also, there are other mechanisms for component

Allee effects driven by resources, natural enemies, and the physical environment that affect both reproduction and survival (Stephens and Sutherland 1999; Berec et al. 2007; Courchamp et al.2008). A variety of different modeling approaches has been used to capture these dynamics for single species (see Boukal and Berec, 2002, for a review), and otherwise (Courchamp et al. 2008, and references therein). Although it seems I may have restricted the scope of both this review and this dissertation with particular assumptions (see Chapter 5), I have illustrated the essential factors that influence the invasiveness of small founder populations under positive density dependence and demonstrated the importance of considering the ecological and evolutionary consequences of Allee effects and intraspecific interactions.

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CHAPTER 2

Allee Effects, Adaptive Evolution, and Invasion Success

Abstract

The mechanisms that facilitate success of an invasive species include both ecological and evolutionary processes. Investigating the evolutionary dynamics of founder populations can enhance our understanding of patterns of invasiveness and provide insight into management strategies for controlling further establishment of introduced populations. Our aim is to analyze the evolutionary consequences of ecological processes (i.e., propagule pressure and threshold density effects) that impact successful colonization. We address our questions using a spatially-explicit modeling approach that incorporates dispersal, density dependent population growth, and selection. Our results show that adaptive evolution may occur in small or sparse populations, providing a means of mitigating or avoiding positive density dependent effects (i.e., Allee effects). The rate at which this adaptation occurs is proportional to the amount of genetic variance and is a crucial component in assessing whether natural selection can rescue a population from extinction. We provide theoretical evidence for the importance of recognizing evolution in predicting and explaining successful biological invasions.

Introduction

While advances in free trade and globalization increase the movement and accelerate the accumulation of invasive species (Lockwood et al., 2005), it is still unclear how introduced populations can successfully establish. As Elton (1958) pointed out, for every successful invasion that occurs, "there are enormously more invasions that never happen, or fail quite soon or even after a good many years" (page 109). What then determines success and failure? This modern biological paradox cannot readily be reconciled, especially in the characteristic case where the founder population is small, since "such populations are definitely in a precarious position" (Mayr, 1965; page 42). Introductions of populations at low density and/or small size are often faced with positive density dependent effects, attributed to demographic stochasticity or reduced cooperative interactions (Courchamp et al., 1999). Allee (1931) first proposed that under these conditions, populations may suffer a decrease in the per-capita rate of increase, from here on referred to as the Allee effect.

Upon arrival in a novel environment, individuals need to overcome a series of challenges in order to reduce the population's risk of extinction. The time period in which this occurs is generally considered the initial establishment phase, and is thought to be a common feature and general pattern of invasion and the process of growth and expansion (Shigesada and Kawasaki, 1997; Sakai et al., 2001). The occurrence of a lag phase that precedes a noticeable increase in population growth and density can result from ecological and/or evolutionary phenomena (Sakai et al., 2001). Small populations that undergo logistic growth slowly increase through the initial phase of the exponential curve, leading to the perception of a time lag. Where this time lag is more pronounced,

populations may be recovering from positive density dependent effects (i.e., Allee effects).

Individuals may suffer a reduction in fitness at low densities for many reasons (reviewed by Courchamp et al., 2008). Even when the initial population is large, rapid dispersal required for expansion could be suicidal as the population density decreases, thereby enhancing positive density dependent effects (Lewis and Kareiva, 1993; Drake et al., 2005; Drury et al., 2007). Commonly, a distinction is made between a 'demographic' Allee effect and a 'component' Allee effect where the population size and density affects the mean overall fitness or some component of individual fitness, respectively (Stephens et al., 1999; Gascoigne et al., 2009). It is often difficult to decipher the exact mechanism that manifests Allee effects (and it is not always the case that component Allee effects lead to demographic Allee effects). Nevertheless, we focus our attention on population level demographic Allee effects with the underlying assumption that a component Allee effect led to the demographic Allee effect. Essentially, it is the case that introduced individuals may be maladapted to small population sizes where their survival and reproductive ability are significantly impacted, and these impacts on individual fitness combine to produce an overall decrease in abundance (i.e., demographic Allee effects). Since Allee effects impact individual fitness, the underlying traits that influence these effects (i.e., component Allee effects) may be subject to natural selection (Courchamp et al., 2008).

Whereas propagule pressure is an emerging explanation for the establishment of invasive species (Lockwood et al., 2005), it relies on an obvious relationship between the number and size of introduction events and the probability of success, since safety in

numbers helps combat Allee effects and stochastic extinction. In the event that propagule size is not large enough to overcome positive density dependent effects, a population may still become established if individuals can adapt to mitigate or avoid Allee effects. Traits that may be responsible for reproductive success and survival at small population densities and sizes include mate finding cues (pheromones and vocal/visual signals), dispersal/aggregation behavior, habitat preferences, mating synchronicity, and gamete morphology and performance (see Courchamp et al., 2008 for detailed studies). Direct evidence for the evolution of these traits as functional adaptations to Allee effects is limited, but we can infer an adaptive evolutionary origin of these traits from studies of sexual selection (Courchamp et al., 2008; Gascoigne et al., 2009).

An evolutionary response to intensive selection pressure imposed by density dependent survival and reproduction relies on genetic variants for adaptive evolution. According to neutral quantitative genetic theory, a loss of genetic variation is expected from population bottlenecks and founder effects (Nei et al., 1975). However it is not neutral variation that matters, but rather evolvability depends on the variation relevant to selection. Maintenance or even increases of this (additive) genetic variation has been theoretically and empirically observed following a bottleneck or in small founder populations (Briggs and Goldman, 2006; Bryant et al., 1986; Cheverud and Routman, 1996; Goodnight, 1988; Turelli and Barton, 2006; Willis and Orr, 1993). Additionally, many recent studies suggest that there is actually no significant reduction in genetic diversity in most successful invaders (Allendorf and Lundquist, 2003; Lee, 2002; Roman and Darling, 2007 and references therein), and that evolution can occur on contemporary timescales (Reznick and Ghalambor, 2001; Carroll et al., 2007; Kinnison and Hairston,

2007). Our purpose here is to explore the feasibility of small populations that may adaptively respond to overcome Allee effects in order to establish, given any amount of genetic variation.

In this paper, we present evidence for the enhanced potential for growth and spread of a small introduced population of organisms faced with Allee effects when adaptation occurs. We model the growth and spread of this population according to a reaction-diffusion equation, and allow evolution to influence positive density dependent effects through a genetic subsystem that provides the opportunity for successful invasion when otherwise (under the current, ecological paradigm) the population would go extinct.

Model Description

The deterministic model that we explore in this paper broadly describes population dynamics with density-mediated growth (i.e., an Allee effect) and diffusive dispersal. This type of demographic model has been used as a compact and tractable representation of invasion (e.g., Skellam, 1951; Lewis and Kareiva, 1993). Specifically, it has been applied to systems such as introductions of nonindigenous freshwater and marine species through ballast water discharge (Drake et al., 2005; Drury et al., 2007). Using this approach, Drake et al. (2005) report acceptable volumes of discharge for various organisms (with differing reproductive rates) for a range of invasion risk tolerances. Here, we consider populations that are introduced below the invasion risk threshold, but nonetheless succeed if evolutionary dynamics are considered in conjunction with the ecological system.

The ecological system

The growth and spread of an introduced population of organisms is represented by a reaction-diffusion equation described by (Lewis and Kareiva, 1993):

$$\frac{\partial u}{\partial t} = ru(1-u)(u-a^2) + D\frac{\partial^2 u}{\partial x^2} \quad (1)$$

which determines the rate of change in the local population density relative to the carrying capacity (u which denotes $u(x,t)$) over time, at a point in space. This equation models the growth of the population (the first term on the right hand side of (1), rhs) at a spatial location that is subject to an Allee effect in addition to migration (which depends on the second term on the rhs of (1)). The diffusion coefficient (D) scales the rate of population spread, in this case across a one-dimensional habitat x. The reproductive rate is regulated by r, and a^2 (which is a function of space and time, derived below) is the local critical density or Allee threshold that determines if population growth is positive or negative (Figure 1a).

There are many variations of single-species models of population dynamics that exhibit Allee effects (see Table 1 of Boukal and Berec, 2002), however the growth function of equation (1) is widely used and flexible (Boukal and Berec, 2002). The behavior of this Verhulst (1838) logistic model modified to include a nonlinear cubic term (based on the Fitzhugh-Nagumo equations; Fitzhugh, 1960; Nagumo et al., 1962), is bistable, with equilibria at $u = 0$ (extinction), $u = a^2$ (unstable threshold), and $u = 1$ (carrying capacity). Figure 1a shows this behavior in terms of the growth of the population (change in population density with respect to time) versus the population density. At densities below the critical threshold (a^2) there is negative population growth declining to extinction (from here on the population is considered extinct below a cutoff density of 0.0001, since a declining population trajectory will only asymptotically

approach zero in a deterministic model; Gomulkiewicz and Holt, 1995); otherwise the population will reach carrying capacity. This is clearly shown in Figure 1b with the graph of the solution of the growth function (population size versus time) at various initial densities.

When diffusion is added to this model of population growth, there are two critical elements that emerge based on the solution to the partial differential equation (PDE). The first is the wave speed, which is determined by the Allee threshold (a^2). Since we are considering a strong Allee effect in this model (i.e., $0<a^2<1$, where the population below this threshold exhibits negative growth versus reduced positive growth from a weak Allee effect), there exists a unique wave speed of the invasion front that is a result of being "pushed" from the inside out, as opposed to being "pulled" by the leading edge (Lewis and Kareiva, 1993). This velocity can be derived through the solution of the PDE (1): $v = \sqrt{2rD}\left(\frac{1}{2} - a^2\right)$ (Lewis and Kareiva, 1993; Murray, 1993). This result suggests that in order for a wave to maintain a positive velocity of advance, the magnitude of the Allee threshold (a^2) must be less than half of the maximum value of the population density relative to the carrying capacity. In addition to the velocity of the wave front, the region occupied by the invading population must exceed a certain critical size for positive growth to occur (Kierstead and Slobodkin, 1953; Skellam, 1951). This phenomenon is clearly explained by Okubo (1980) by noting that whereas reproduction takes place within a region or patch, diffusion takes place at the boundaries resulting in a loss of organisms, thus reducing the density within the patch. This tradeoff in the ratio of inner region volume to outer surface area will either allow a population to grow or decline with an inverse relationship of diffusivity to rate of growth. This relationship gives a

minimum region within which reproduction cannot compensate for loss due to diffusion, especially when Allee effects influence population growth. Thus, Lewis and Kareiva (1993) derive a minimum size condition (i.e., the radius of the initial beachhead) based on the wave speed that is required for the population to establish and radially expand. We address this critical size threshold qualitatively, as the analytical solution (i.e., $R_{\min} > \left(\frac{D}{2r}\right)^{\frac{1}{2}}\left(\frac{1}{1/2 - a^2}\right)$; Lewis and Kareiva, 1993) is for two-dimensional spread, while we work with a simpler one-dimensional model. The minimum critical radius is proportional to the ratio of diffusivity (i.e., diffusion coefficient, *D*) to the reproductive rate (controlled by *r*). The inclusion of diffusion in the model provides a spatially explicit understanding of how all of the components interact to affect invasion/establishment success. The diffusion process has been extensively analyzed in invasion processes (e.g., Fisher, 1937; Skellam, 1951; Okubo, 1980).

The evolutionary subsystem

In order to incorporate evolutionary factors that may influence invasion success, we develop a quantitative genetic subsystem. This genetic subsystem is coupled to the ecological model to explore the effects of selection and genetic variance on traits that may increase a population's likelihood of survival. Specifically, we allow the Allee threshold to become a dynamic parameter that is considered to be a fitness related trait (e.g., a trait impacting the component Allee effect). From here on, except in the absence of evolution, referring to the Allee threshold implies that that value is the initial value, since it changes over time. This quantitative trait influences an organism's ability to survive and reproduce in a small population. The results reveal the possibility that an

introduced population that would fail to persist in the ecological context of this model has the potential to succeed through evolutionary means. Including evolution within the context of ecological invasions can serve to provide more robust predictions for management strategies. Therefore, it is important to investigate the possibility of evolution in the analysis of invasions.

The framework that is used to link evolutionary change with ecological processes involves developing a relationship between the fast, ecological and slow, evolutionary timescales in order to make these rates comparable (Kondrashov and Khibnik, 1996). In the coupled evolutionary ecology model, the reaction-diffusion equation (1) describes the change in the population density over time and is tied into a genetic subsystem that allows the organismal response to population density to evolve in terms of the selection gradient and genetic variance. Since the population dynamics vary across space, the genetic subsystem describes the rate of change of the trait mean (i.e., the Allee parameter) at each location *x* by:

$$\frac{\partial a}{\partial t} = \varepsilon \frac{\partial f(u,a)}{\partial a} + 2D \frac{\partial a}{\partial x} \frac{\partial \ln(u)}{\partial x} + D \frac{\partial^2 a}{\partial x^2} \qquad (2)$$

(Pease et al., 1989; Kirkpatrick and Barton, 1997; Garcia-Ramos and Kirkpatrick, 1997; Hare et al., 2005). The first term on the right hand side reflects the force of local directional selection, where the selection gradient for frequency-independent selection is the rate of change of the mean Malthusian fitness function (i.e., per-capita growth rate: $f(u,a) = r(1-u)(u-a^2)$) with respect to the trait, *a* (Lande, 1976; Falconer, 1989). Thus, $\frac{\partial f(u,a)}{\partial a} = 2ra(u-1)$, where we assume that individual fitness approaches the population mean fitness, since most individuals are close to the average phenotype

(Webb, 2003). This suggests that the genetic variance (ε) is small (and constant in this model). This small parameter for the genetic variance can be used to couple the fast ecological timescale, t, with the slow evolutionary timescale, $\tau = \varepsilon t$ (Kondrashov and Khibnik, 1996; Webb, 2003). Combing these two components of genetic variance and selection, quantifies the effect of natural selection on the local mean value of the quantitative trait (the Allee parameter; Lande, 1976; Falconer, 1989).

In order to account for the influence of migration on the trait's local mean, the latter two terms in equation (2) incorporate space. The middle term takes into account asymmetrical gene flow caused by the variation of density across space (Pease et al., 1989; Kirkpatrick and Barton, 1997; Garcia-Ramos and Kirkpatrick, 1997; Hare et al., 2005). This captures the influence of the mean trait value (i.e., genetic contribution) from more abundant populations to less abundant neighboring locations due to the spatial gradient, since more individuals migrate from areas with relatively high population densities. The last term mirrors the diffusion term from the ecological model, and describes the homogenizing effect of random dispersal.

We solved the spatially explicit system numerically using MATLAB 7.0 (R14) using a finite difference method to incorporate diffusion and gene flow (adapted from Garvie, 2007). By iterating equations (1) and (2) forward in time, the population density and Allee threshold at each location are updated with diffusion following growth and selection, respectively, while incorporating the spatial gradient. The simulated populations, with and without evolution, behaved as we expected from the model equations ((1) and (2)), and adequately approximate/represent the critical conditions that govern this dynamical system.

Results

The dynamics of the evolutionary ecology model can be interpreted using the idea of fast and slow timescales (Kondrashov and Khibnik, 1996; Webb, 2003). Earlier, we assumed that the genetic variation (ε) was small (to use mean fitness as a proxy for individual fitness), which can subsequently be taken advantage of for our analysis of the coupled evolutionary ecological dynamics. When $\varepsilon = 0$, the situation without evolution, the genetic subsystem is frozen and the population moves towards a stable equilibrium of the ecological subsystem (carrying capacity or extinction) depending on its initial density (greater than or less than the Allee threshold respectively; Figure 1b) and initial radius (spatial extent) in the spatially explicit model. When $\varepsilon > 0$ but small, the Allee threshold evolves relatively slowly and influences the ecological system. Whenever the population is below its carrying capacity ($u = 1$ for each spatial coordinate x when space is explicit), equation (2) is negative, and decreases the mean Allee threshold (a^2), since the intensity of selection is density dependent. Thus, fitness increases as Allee effects are suppressed, and selection drives the Allee threshold towards zero. If the population density is greater than the Allee threshold, but still below the carrying capacity, it will progress towards carrying capacity more rapidly than it would without evolution as a^2 decreases; since the rate at which the population density changes (equation (1)) is proportional to the difference between u and a^2. The ecological dynamics are reversed when the population density is below the Allee threshold since the population declines towards extinction, but more slowly than it does without evolution. When $u < a^2$, equation (1) is negative, and the population density approaches extinction more rapidly with a^2 constant (since the difference between u and a^2 increases), than it does with evolution as a^2 decreases

(revealing a more pronounced time lag to extinction). During this time lag, as the population slowly declines, the opportunity for evolution to overcome positive density dependent effects occurs. If the rate of evolution is fast enough, the Allee threshold can fall below the population density, causing the rate of change of population density to become positive (where $u > a^2$) and the population grows and can successfully invade . The chance that evolution can rescue the population from extinction depends on the relative rates of genetic change in the quantitative trait (i.e., Allee threshold) and of population decline (Gomulkiewicz and Holt, 1995); hence the amount of genetic variance greatly impacts the ability to adapt and survive.

A non-spatial example of this process, referred to as evolutionary rescue (Gomulkiewicz and Holt, 1995), is shown in Figure 2, where a population is introduced below the Allee threshold. Without evolution, the population declines to extinction (Figure 2a, solid line) as the Allee threshold remains constant (Figure 2b, solid line). When the population can evolve (Figure 2, dotted line), it declines at first until it can overcome the magnitude of positive density dependence, and is then able to successfully establish. As it is difficult to measure the Allee effect empirically (Tobin et al., 2007), we use an extreme value that exaggerates density dependent effects in order to investigate the 'worst case scenario' ($a^2 = 0.3$, where the population exhibits deterministic decline when its density is less than 30% of its carrying capacity). When evolution is included, we used a small value for the genetic variance, $\varepsilon = 0.02$, in order to remain consistent with fast-slow dynamics, unless otherwise indicated.

In general, there is a range of parameter space that permits persistence for a population below the Allee threshold in the non-spatial model with evolution (instead of

simple decline to extinction). We explored this behavior while varying the genetic variance from zero to 0.1. As genetic variance increases, we are essentially relaxing the assumption of fast-slow timescales and allow evolution to occur more rapidly. These dynamics are shown in Figure 3 where initial population densities below the Allee threshold require a minimum amount of genetic variance in order to avoid extinction. In this case, the rate of reproduction, r, also influences the potential for evolutionary rescue, since it impacts both population growth and rate of evolution (equations (1) and (2), respectively). As we relax the assumption of fast-slow timescales, the behavior remains qualitatively the same as that described analytically under a strict fast-slow timescale assumption.

Including more realistic population dynamics through spatial structure provides further invasion criteria. Nonetheless, the additional complexities result in qualitatively similar behavior to the non-spatial model. In this case, not only will evolution influence population growth, it affects the wave speed and the critical size threshold, $R_{\min}$. As the population overcomes Allee effects with a decreasing Allee threshold, the wave speed accelerates and the critical patch size becomes smaller. Thus, in addition to the initial density of the introduced population and the genetic variance, the initial radius or patch size of the initial invasion area, the ratio of diffusion to reproduction, and gene flow will factor into successful establishment and give rise to a wider range of interactions between the ecology and evolution of this system.

The numerical solution of equation (1) (without the evolutionary subsystem) in one-dimensional space, with an initial population density below the Allee threshold, declines to extinction (Figure 4a). This is contrasted by the results when the evolutionary

subsystem is included. With the initial population density below the Allee threshold, Figure 4b shows that the population rebounds from decline. The same type of rescue occurs for a population that starts near carrying capacity, but occupies an initial spatial size below that which is necessary for a population to successfully establish. Figure 5a shows a rapidly declining population that goes extinct. Under the same circumstance, but where evolution of the Allee threshold occurs, Figure 5b shows the population density at first beginning to shrink and then growing and expanding. In addition to the time evolution of population density across space in Figures 4 and 5, the evolution of the mean trait value across space illustrates how gene flow and the density dependent selection gradient influences its rate of change and distribution (Figures 4c and 5c). Since the intensity of selection is density dependent (and we assume constant genetic variance), locations with smaller populations can evolve the trait value more rapidly compared to other areas where Allee effects may not be as strong and experience weaker selection. The trait distribution over time, Figures 4c and 5c, therefore reflect the population density distribution, but are also influenced by the trait values of the migrants. As individuals disperse out to new locations and push the boundaries of the species range, their trait values are averaged to determine the demographic Allee threshold for that spatial coordinate. This demographic Allee threshold combines with their local population density to influence individual fitness and population growth (where the distance between the density and mean trait value is the initial degree of maladaptation).

We explored when evolutionary rescue occurred across a range of parameter values for the spatially explicit model. According to Drake et al. (2005), variability among locations and over time makes it unreasonable to determine precise estimates for

the diffusion coefficient, D. We therefore explored a range of values, and present those that best illustrate breadth of behavior. The parameter that controls the reproductive rate, r, was also varied substantially, but since the spatial dynamics depend on the ratio of diffusion to rate of reproduction (resulting in a measure of length); we fixed r and varied D, unless otherwise noted. This was justified since the results of the spatial simulations are qualitatively identical for equivalent ratios. The effects of the critical patch size, initial population density, ratio of diffusion to growth and genetic variation on evolutionary rescue and population dynamics are shown in Figure 6.

When the size of the initial population is too small (i.e., a radius of 1), a population at carrying capacity (i.e., $u = 1$) will go extinct without evolution due to the relative effect of diffusion to reproduction (Figure 6a). If evolution occurs rapidly enough (i.e., $\varepsilon > 0.02$), the population can overcome positive density dependent effects and compensate for the loss due to diffusion and rebound from low densities. When the initial radius of the population is increased (Figures 6b and c), the chance of survival and establishment (growth and expansion) of populations above or below the Allee threshold increases with initial density and genetic variance. Therefore, the initial radius of the population can significantly impact the likelihood of evolutionary rescue for populations with the same amount of genetic variance.

This is demonstrated further in Figure 7a, where the rate of recovery (i.e., the inverse of the time lag before growth becomes positive and the population reaches carrying capacity) for a population near carrying capacity depends on its initial size/radius and genetic variance. Where size and variance are small, rescue never occurs. As these parameters increase, the rate of recovery gradually becomes faster until it

essentially plateaus (although with greater variance and initial radius, the rate of recovery may slow slightly if the initial spatial extent is large enough for the population to experience early growth before diffusion causes decline prior to recovery). If the population occupies a large enough spatial extent, it will succeed without evolution (where the genetic variance is zero), however the lag time may be more pronounced depending on the ratio of diffusion to reproduction through the tradeoff between growth and spread (e.g., if spread is relatively fast compared to reproduction, $D/r = 1$). The population density may thus initially decline across space until reproduction can sufficiently overcome the loss due to diffusion, and the population can grow to carrying capacity. Similar to the non-spatial case, a population (greater than the Allee threshold) above the spatial threshold will grow to carrying capacity more rapidly with evolution than without.

As shown in Figure 7b, when evolutionary rescue is possible, the initial level of maladaptation ($a_0^2 - u_0$) and the genetic variance (ε) also determine the rate at which evolutionary rescue proceeds. Figure 7b uses parameters (i.e., radius and ratio of D to r) for a population that would decline and go extinct without evolution regardless of the initial density. Hence, it is clear that the amount of time required for a population to begin growing depends on its initial level of maladaptation (to both the critical density and spatial thresholds) and/or genetic variance. Since the rate at which this rescue occurs depends on the amount of genetic variance (equation (2)), it may take an extremely long time (as $\varepsilon \rightarrow 0$, the rate of recovery $\rightarrow 0$) for the Allee threshold to fall below the population density. In this circumstance, as the population density becomes very close to zero, the rate of change of the Allee threshold is greater than that of the population

density (as $u \to 0$, $\partial u / \partial t \to 0$ and $\partial a / \partial t \to -2\varepsilon r a$). Thus, theoretically, rescue would always occur (Gomulkiewicz and Holt, 1995). However, to maintain biological realism, when solving this system numerically, we always considered the population extinct when the maximum density (across space, when diffusion is included) becomes reasonably close to zero (i.e., $u = 0.0001$; we chose this protocol instead of the total population across space due to the diffusion dynamics based on the Gaussian dispersal kernel and the "pushed" wave front behavior).

Overall, the numerical results qualitatively hold for a wide range of dimensional parameter values and initial conditions with and without diffusion and in one- and two-dimensional space. Results for two-dimensional space are not shown since they are qualitatively similar to the simpler, one dimensional model.

Discussion

From these results, it is apparent that adaptations that enable organisms to overcome the negative effects of low densities can allow the population to rebound from a trajectory toward extinction to grow to reach carrying capacity. Current management strategies (e.g., reducing population density or size) are based on ecological theory (e.g. Drake et al., 2005), but this evolutionary ecology model suggests that adaptive evolution can enable successful establishment and that ecological considerations alone may not be sufficient.

Under the assumptions of an Allee effect and diffusive dispersal, the idea of ecological size thresholds fits well with the ecological evidence that a large founding population is a primary cause of successful establishment (Lockwood et al., 2005; Colautti et al., 2006). However, by incorporating evolution, we see that the situation is

not quite this simple because ecological size thresholds and genetic variance can interact to determine successful establishment. As the ratio of diffusion to reproduction decreases, the spatial constraint on population growth becomes weaker, and less genetic variance is needed to rescue populations with densities below the Allee threshold. As the initial spatial radius of introduction increases, population persistence is more likely with less genetic variance for selection to act on. Furthermore, the rate of this rescue depends on the initial genetic load or maladaptation (i.e., how far the population density is from the Allee threshold), as well as the amount of genetic variance. Because bottlenecks during founding events do not always result in highly reduced genetic variability, even small founding populations may have sufficient genetic variation to evolve to overcome Allee effects and establish, contrary to solely ecologically based predictions.

Additionally, we can draw several general insights about how dispersal impacts selection and evolution of Allee effects in an invasion context. As species are transported from their native environment into novel habitats or simply disperse on their own, it is clear that the genetic composition of the local population can influence the rate of evolution and adaptation to the new local conditions. Given enough genetic diversity, local populations can adapt to their local environment, but dispersal may hinder survival across ecological clines as dispersers tend to be maladapted to the new local environment. Essentially, local population persistence depends on the race between the rate of evolution and the degree of maladaptation (Gomulkiewicz and Holt, 1995). In this case, gene flow will play a major role in determining the outcome. As Kirkpatrick and Barton (1997) and Garcia-Ramos and Kirkpatrick (1997) demonstrate, individuals moving from one selection regime from the center of their species' range to the periphery can introduce

enough maladaptation that the new area becomes a sink environment. On the other hand, Holt et al. (2004) show that immigration can have a positive influence on adaptation to sink environments, in some circumstances. Resolving the disparity between these perspectives requires understanding what is contributing to the severity of maladaptation and the population's ability to overcome it.

In our model, dispersal impacts survival ecologically through the critical patch size, and genetically, since individuals may move from areas where they are better-adapted (i.e., the population density is greater than the Allee threshold or mean trait value) to sink regions, where they are maladapted. As individuals disperse across space, they may be contributing positively in an ecological sense to the quality of their new local environment (by increasing the local population density). However, dispersers are more likely to come from higher density areas where Allee effects, and hence selection, are locally weak. These dispersers potentially introduce more maladaptation to their new location, because they increase the average phenotype (Allee threshold) in the new location where density is likely to be lower.

Interestingly, the evolutionary impacts of migration in this model do not dramatically influence the dynamics. Changes to the local mean phenotype through local selection and simple mixing (i.e., diffusion) actually slightly hastens the evolutionary rescue effect over a model that considers only the impact of local selection. Since the selection intensity is density dependent and proportional to u - 1 for each point in space, the peripheral individuals faced with stronger selection with lower trait values have a small positive influence on the more dense neighboring populations. The gradient term accounts for asymmetric gene flow due to differential migration from areas of relatively

high population densities. However, this term does not alter the overall evolutionary dynamics based on local selection any more than adding the diffusion term, since the negative effects of gene flow and the local rate of evolution (which is relatively fast, based on the selection intensity) essentially cancel each other out. In this context, similar to that of Holt et al. (2003, 2004), the immigrants simply contribute to the local population density, which helps prevent extinction long enough for evolutionary rescue to occur locally (i.e., positive population growth; note that whereas Holt et al. (2003) attribute the main effect of immigration to the contribution of variation, this is not the case in our model, since we assume constant genetic variance). Overall, our results are similar to that of Holt et al. (2004) where immigration has a demographic effect on increasing fitness that can essentially outweigh the 'swamping' effect of gene flow.

In general, the primary determinant of invasion success depends on positive population growth at the center of the introduced range. This result comes from the Allee effect (and the solution to the partial differential equation (1)) by forcing a "pushed" travelling wave front (Lewis and Kareiva, 1993), where the wave speed causes population expansion, contraction, or propagation failure (i.e., pinning; Keitt et al., 2001). Intuitively, aggregation-like behavior emerges based on the strength of the Allee effects. Individuals that disperse too far from the whole are likely to die before they can "pull" others in their vicinity. In this regard, growth occurs from the inside out, where the population seemingly spills out and overflows to expand its range. Consequently, in this study, and for biological invasions that exhibit similar dynamics, it is more important to focus on the center of the invader's range and whether the initial beachhead can survive (through evolutionary rescue), than the fate of peripheral populations at the wave front

when determining the importance of evolution on invasion success. This is also understood by comparing the non-spatial (Figure 3) with the spatial (Figure 5) sensitivity analysis. The overall dynamics are qualitatively similar in the parameter space that allows for evolutionary rescue to occur.

Even though gene flow and spatial structure do not dramatically influence the establishment of an introduced population, additional invasion criteria need to be considered. When analyzing the model behavior in a spatially explicit context, there is an ecological tradeoff between growth and spread that affects establishment and the rate of recovery. As previously mentioned, reproduction needs to compensate for the loss due to diffusion. Including evolution and suppressing Allee effects, actually contributes to the acceleration of the wave front (i.e., enhancing dispersal speed). A population then can more rapidly disperse as it evolves, and may become more of an invasion threat as long as this range expansion does not reduce their density too quickly. Whereas this increasing wave speed can lead to a slightly longer lag phase prior to positive population growth, the population will likely be inevitably rescued because this effect primarily influences the dynamics at the periphery and is offset by the reduction in the critical invasion area ($R_{\min}$). Although there is no range contraction (since there is always a positive wave velocity with unbounded expansion due to the parameter values and absence of environmental heterogeneity or range limitations; Filin et al., 2008), as the critical patch size ($R_{\min}$) becomes smaller with the decreasing Allee threshold, rescue occurs more readily at the range center as the critical patch size threshold criteria weakens and the behavior approaches that of the non-spatial model. This may seem like an oversimplification of the global dynamics; however these conclusions are valid in the

context of this investigation which focuses on the establishment phase rather than subsequent range expansion and spread.

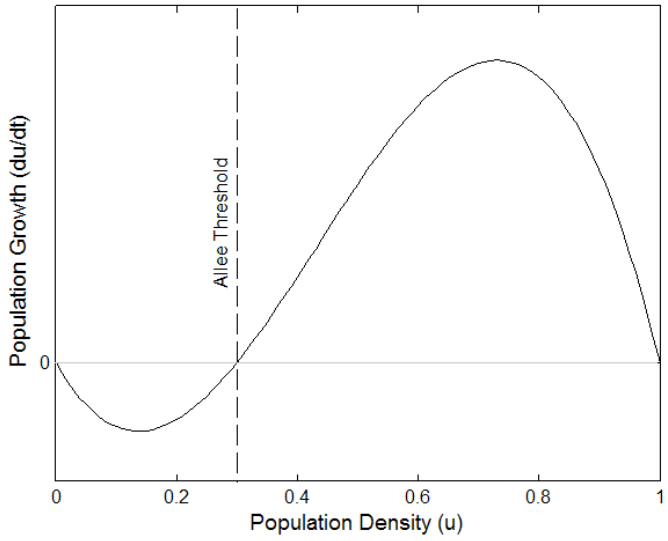
Recognizing that evolution can significantly affect the establishment success of invasive species is becoming more widely accepted, influencing the ways in which invasion biologists conduct their research (see the other articles in this issue). Specifically, adaptations that diminish Allee effects and evolutionary responses to density dependence are beginning to emerge as viable explanations for sustaining vulnerable populations at low density and size (Gascoigne et al., 2009). Since it is difficult to conclusively support this claim empirically (as the origin of the adaptation or the associated cost may be unknown; Courchamp et al., 2008; Gascoigne et al., 2009), mathematical models that incorporate evolution and compare the effects of various strategies (e.g., mitigating component Allee effects) can help decipher the mechanisms that both limit and facilitate population growth. Two such models that incorporate adaptations to component mate-finding Allee effects compare the efficiency and survival of populations at various densities that attract mates with or without a sexual pheromone (Jonsson et al., 2003) or by increasing mate detection distance (Berec et al., 2001). Another study suggests that broadcast spawners that evolve their gamete morphology and performance under sperm limitation (at low density) bear a cost of decreased fitness at high density due to hybridization and competition (Levitan, 2002). In these cases, particular strategies are shown to influence population viability in addition to an associated tradeoff, whereas our investigation provides broad, albeit simplistic, results dealing with generalized demographic Allee effects and evolution.

In order to understand how the results of this simplistic model extend to more realistic and complex evolutionary scenarios, spatially explicit, individually-based stochastic simulation of the introduced populations should be developed to investigate more closely the mechanisms that allow these population level dynamics to emerge. In particular, tracking the mean value of a component Allee effect is sufficient to illustrate how evolution can overcome positive density dependence and result in invasion. However, this approach may not be sufficient to make the specific quantitative predictions necessary for management of invasive species. This is due to the simplifying assumption of constant genetic variance based on mutation-selection balance (Lande, 1976). Complex simulations could relax this assumption and permit genetic variation to change via mutation, selection, and drift, in tandem with the demographic processes in a heterogeneous environment, and explicitly investigate the costs associated with avoiding Allee effects. Hence, future models should incorporate how propagule pressure (size and frequency of introduction events) impacts genetic variation and how more realistic genetic architectures contribute to the evolutionary trajectory of invasive species.

Although there is still much more work to be done to elucidate the factors that determine establishment success of founder populations, this theoretical approach has the promise to provide evidence in support of our working hypothesis that adaptive evolution can mitigate Allee effects and be an important driver of biological invasions.

Figure 1: Growth dynamics of the model population (a), and the solution of equation (1) without diffusion (b) with reproductive rate, $r = 0.6$, and Allee threshold, $a^2 = 0.3$. Trajectories for population size (b) are given for initial densities from 0 to 1 in increments of 0.05.

(a)



(b)

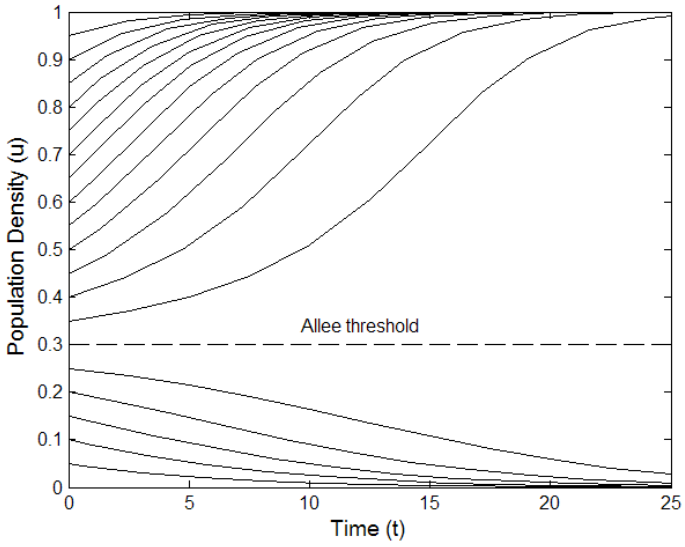
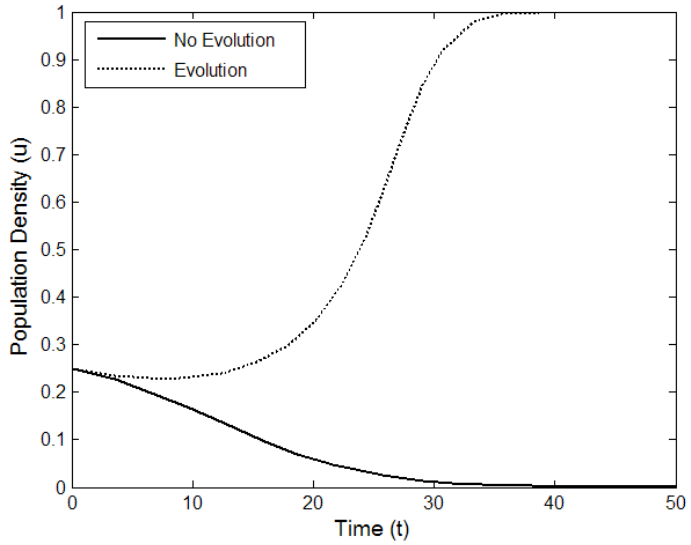


Figure 2: Comparison of an invading population introduced at a density below the Allee threshold, $a^2 = 0.3$ ($u = 0.25$, $r = 0.6$). The solid line represents the non-spatial system ($D = 0$) described by equations (1) and (2) without evolution ($\varepsilon = 0$) which results in extinction (a) and a constant Allee threshold (b). The dotted line indicates population growth (a) when evolution ($\varepsilon = 0.02$) acts to reduce the Allee threshold (b).

(a)



(b)

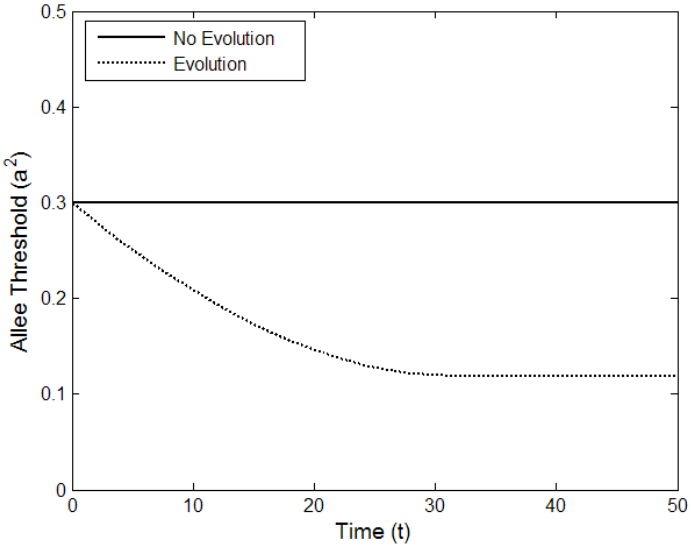


Figure 3: Parameter combinations of reproductive rate, r, genetic variance, ε, and initial population density, u, that result in extinction or evolutionary rescue. In this non-spatial scenario, initial population densities greater than the Allee threshold ($a^2 = 0.3$) always succeed, thus the focus is on the parameter space that allows for evolutionary rescue (i.e., where the population growth changes from negative to positive). As the reproductive rate increases from 0.1 to 1, there is less genetic variance needed for a population to evolve to overcome positive density dependence since increased reproduction will contribute to suppressing Allee effects.

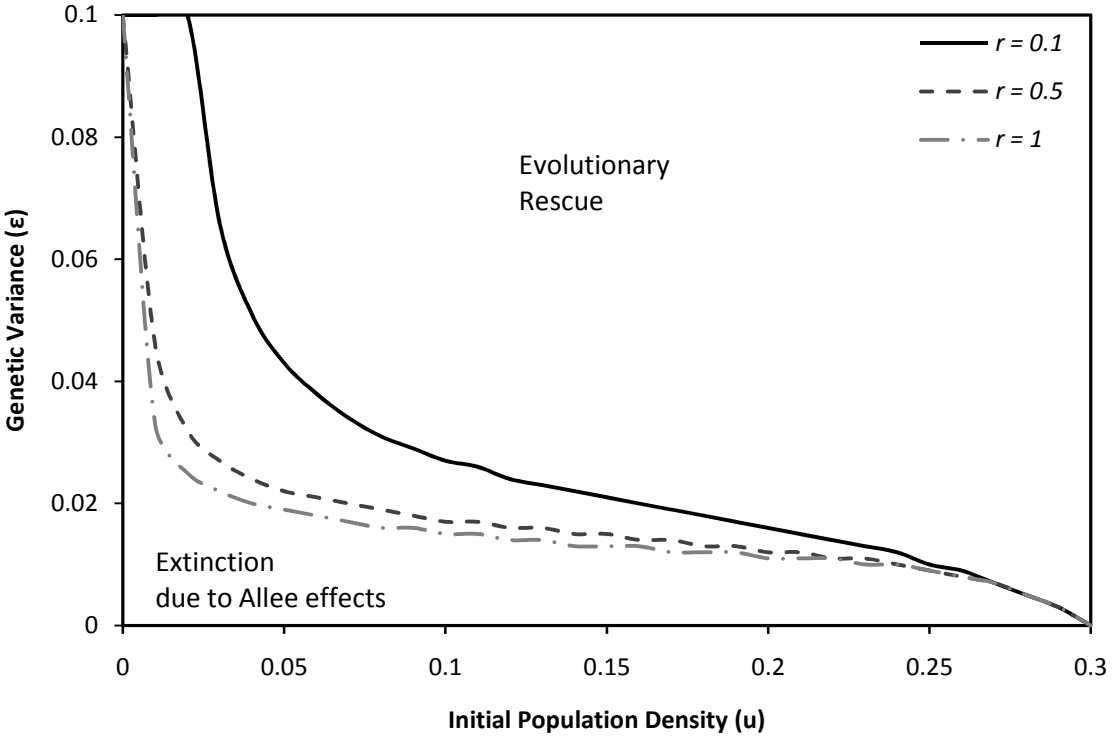
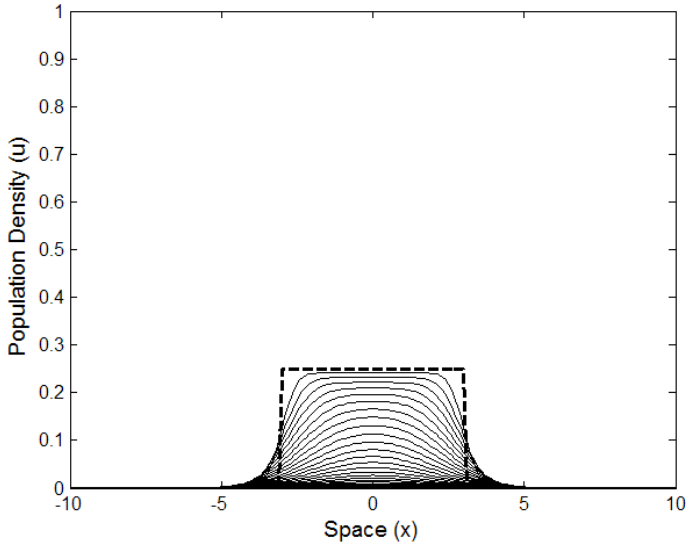
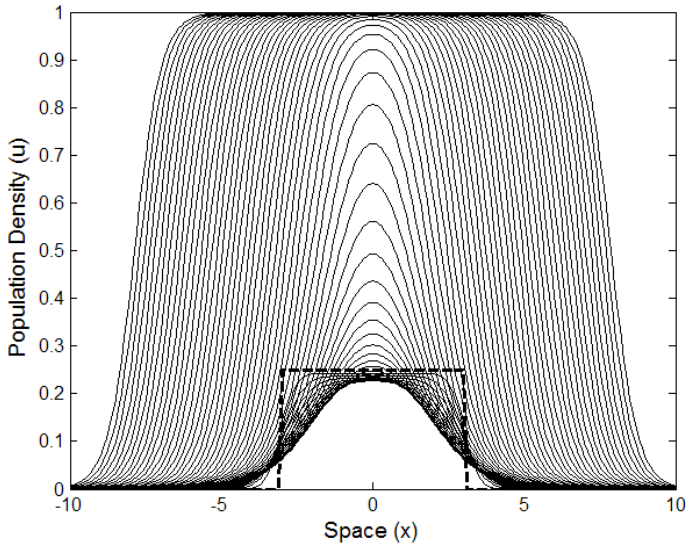


Figure 4: Diffusive dispersal of an introduced population at an initial density (bold dashed line) below the initial Allee threshold, $a^2 = 0.3$ ($u = 0.25$, $r = 1$, $D = 0.1$) across a linear, one dimensional habitat. The population collapses over time to extinction (a) where there is no evolution ($\varepsilon = 0$), and succeeds (b) after an initial decline with evolution ($\varepsilon = 0.02$). (c) shows the evolution of the mean value of the Allee threshold across space (where the initial distribution is given by the bold dashed line). The population density distribution and corresponding trait values (i.e., Allee threshold) are plotted at equal time increments (every 20 of 1200 model iterations).

(a)



(b)


Population Density (u)
Space (x)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-10
-5
0
5
10

(c)

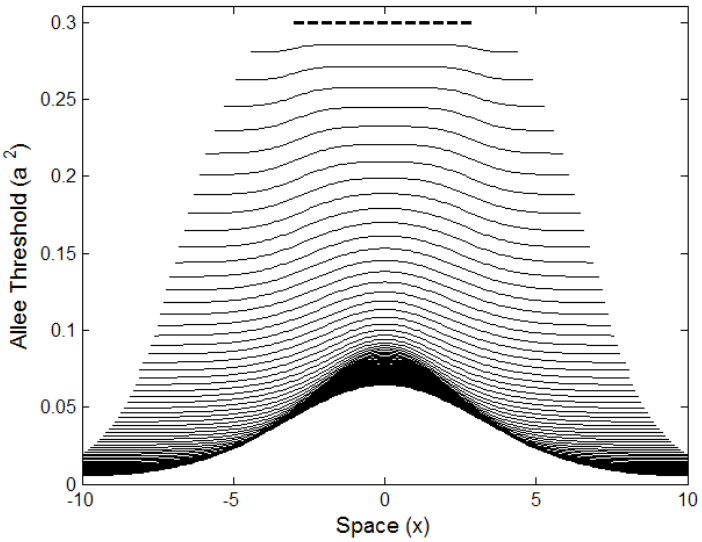
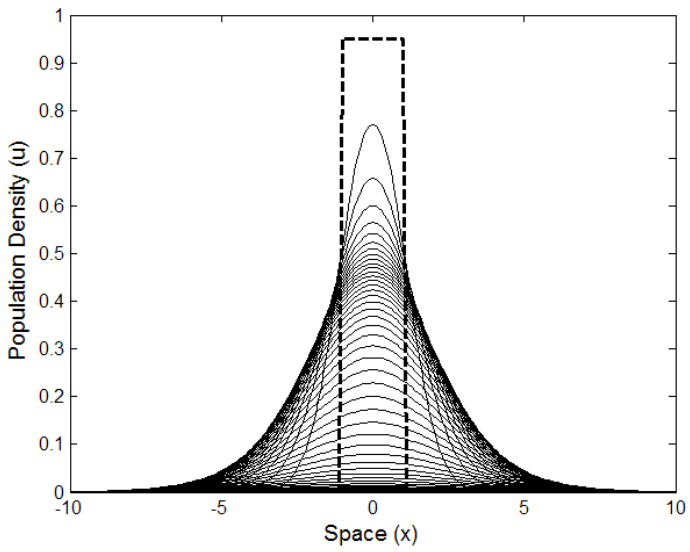
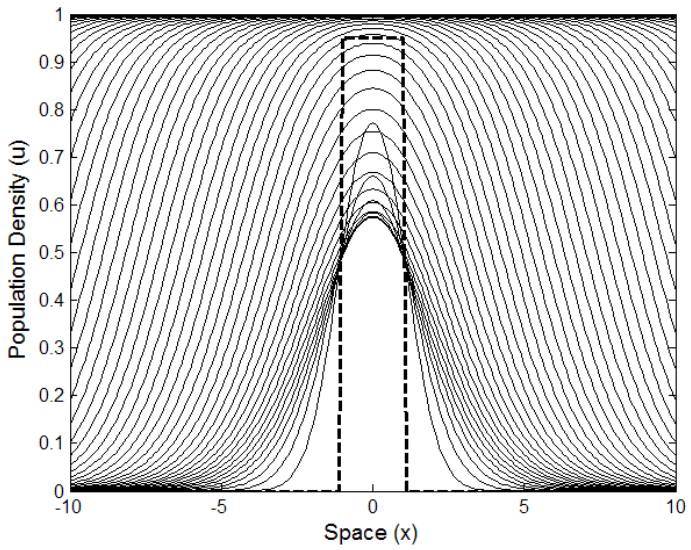

Allee Threshold (a 2)
Space (x)
0.3
0.25
0.2
0.15
0.1
0.05
0
-10
-5
0
5
10

Figure 5: Population density of a diffusion dispersed population across one dimensional space. The initial population density (bold dashed line) is near carrying capacity (u = 0.95, a^2 = 0.3, r = 1, D = 0.5), but introduced below the minimum radius of area determined to be critical for invasion success. (a) is collapsing to extinction without evolution (ε = 0), whereas (b) shows success of an invader with evolution (ε = 0.02) after initial decline. (c) shows the evolution of the mean value of the Allee threshold across space (where the initial distribution is given by the bold dashed line). The population density distribution and corresponding trait values (i.e., Allee threshold) are plotted at equal time increments (every 20 of 1200 model iterations).

(a)



(b)


Population Density (u)
Space (x)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-10
-5
0
5
10

(c)

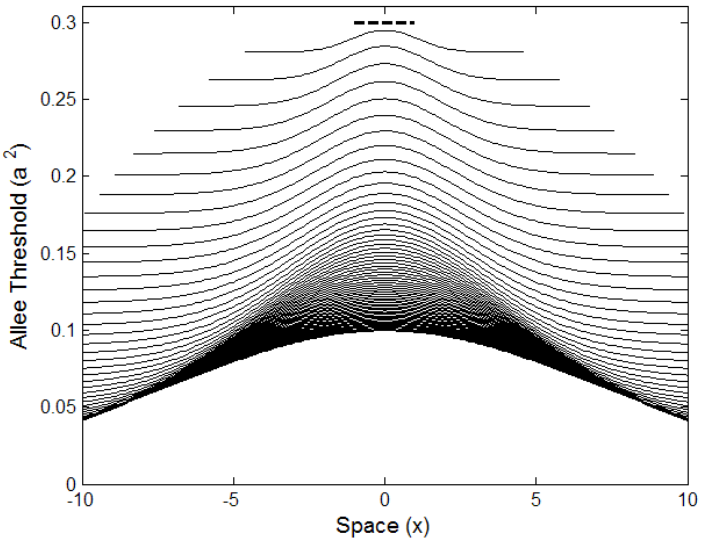
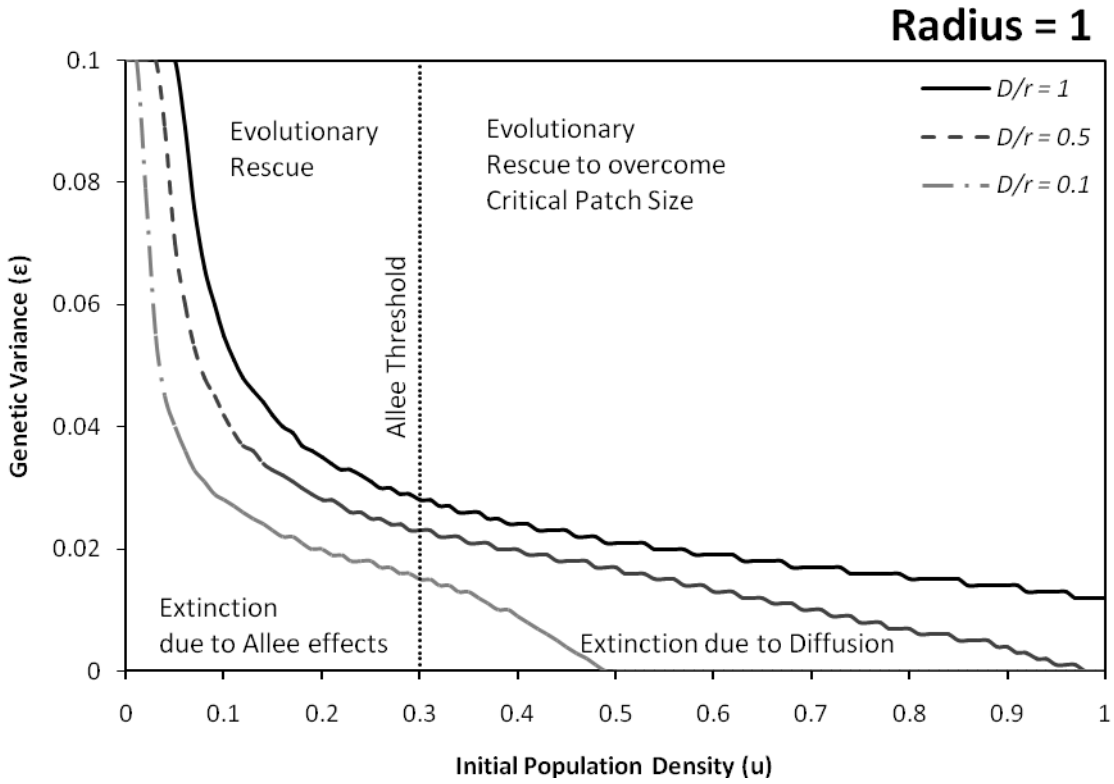
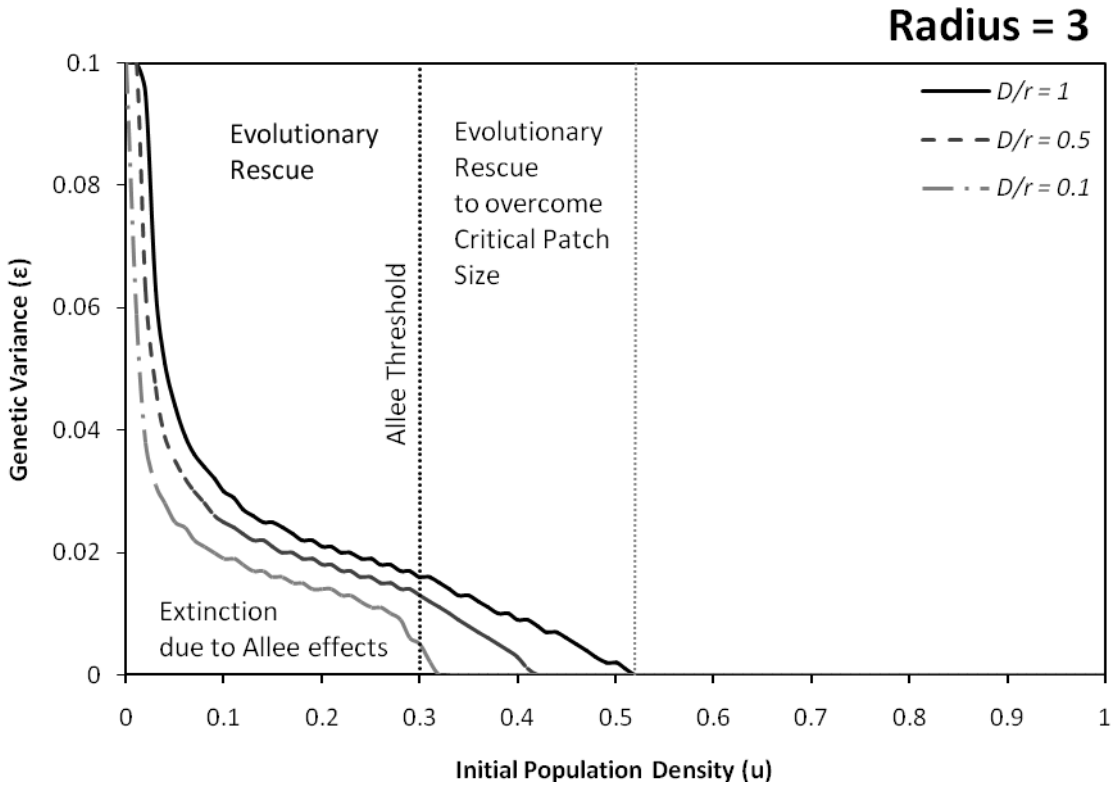

Allee Threshold (a 2)
Space (x)
0.3
0.25
0.2
0.15
0.1
0.05
0
-10
-5
0
5
10

Figure 6: The sensitivity of population growth and expansion based on the combination of parameter values. The ratio of the diffusion coefficient (D) to the reproductive rate (r) determines whether the population will expand or collapse according to the initial radius of the introduced population. The areas under the curves denote combinations of genetic variance and initial population density that result in extinction. Areas above the curves are combinations of genetic and/or demographic conditions that produce inevitable persistence. The parameter space between the vertical dashed lines refers to the different ways population survival is influenced. To the left of the initial Allee threshold, the initial population density will either go extinct due to density dependent effects (below the D/r curve), or given enough genetic variation, will be evolutionarily rescued (above the D/r curve). The area to the right of the initial Allee threshold (and between the dashed lines in (b) and (c)) is the case where the initial population density is greater than the Allee threshold but due to the initial spatial size and the ratio of diffusion to reproduction, the population may go extinct without sufficient genetic variance (below the D/r curve), otherwise it will evolve to overcome the critical patch size effect. For initial population densities greater than the rightmost dotted line, populations persist solely due to ecological effects. Thus, the area between the dashed lines in (b) and (c) truly delineates evolutionary rescue when $D/r = 1$. The rightmost vertical line moves slightly to the left to the point of intersection of the D/r curve and the x-axis for other values of D/r. Graphs (a), (b), and (c) represent different radii of the linear habitat that the introduced population initially occupies.

(a)


Radius = 1
D/r = 1
D/r = 0.5
D/r = 0.1
Evolutionary Rescue
Evolutionary Rescue to overcome Critical Patch Size
Allee Threshold
Extinction due to Allee effects
Extinction due to Diffusion
Genetic Variance (ε)
Initial Population Density (u)
0
0.02
0.04
0.06
0.08
0.1
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

(b)


Radius = 3
D/r = 1
D/r = 0.5
D/r = 0.1
Evolutionary Rescue
Evolutionary Rescue to overcome Critical Patch Size
Allee Threshold
Extinction due to Allee effects
Genetic Variance (ε)
Initial Population Density (u)
0
0.02
0.04
0.06
0.08
0.1
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

(c)

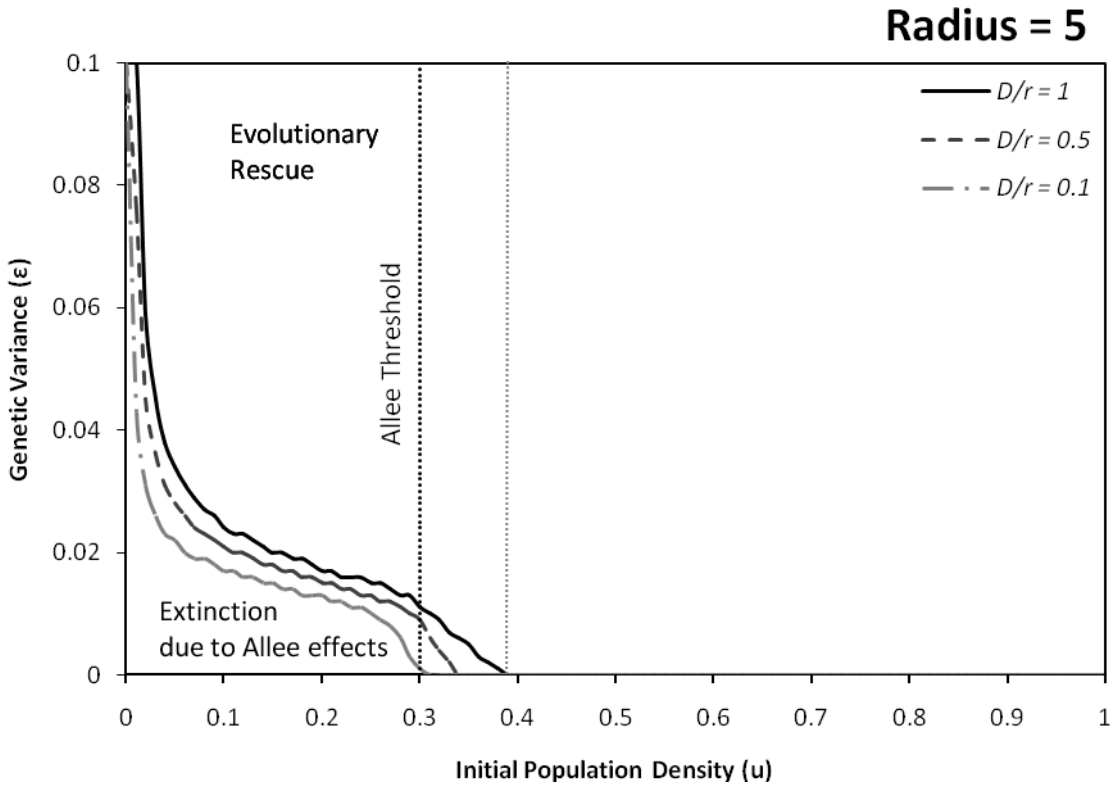
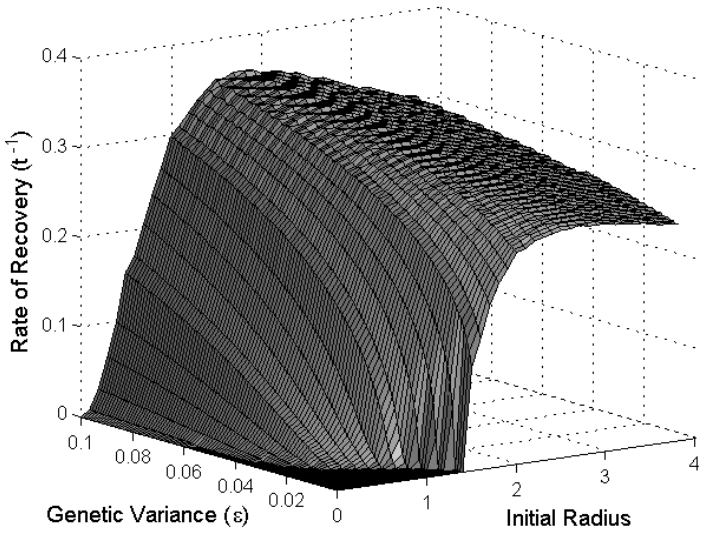
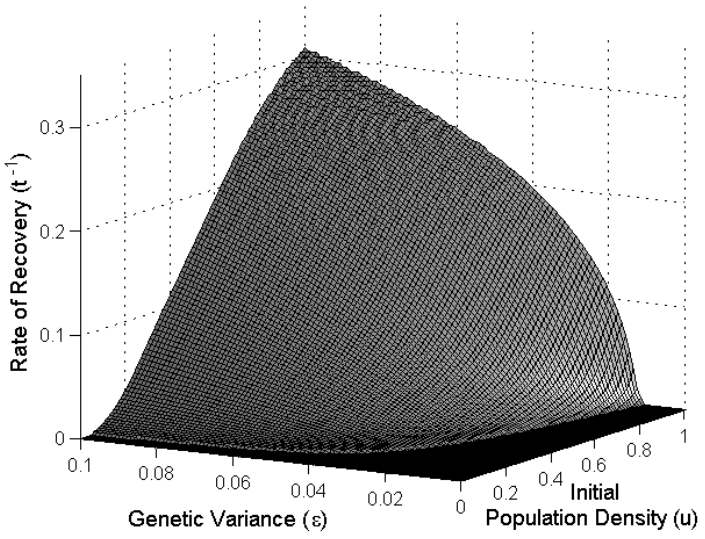

Radius = 5
D/r = 1
D/r = 0.5
D/r = 0.1
Evolutionary Rescue
Allee Threshold
Extinction due to Allee effects
Genetic Variance (ε)
Initial Population Density (u)
0.1
0.08
0.06
0.04
0.02
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

Figure 7: Rate of recovery in terms of the inverse of the time lag before population growth becomes positive, where one "timestep" equals 24 iterations of the model. In (a), the initial population density is near carrying capacity (u = 0.95, a^2 = 0.3, D/r = 1), and the initial radius and genetic variance, ε, varies. Where the rate of recovery is zero, the population goes extinct since it initially occupies an area smaller than the critical patch size (in this case, a radius of 1.4) or does not have sufficient genetic variance to evolve quickly enough to be rescued prior to extinction. Increasing the genetic variance and initial radius will decrease this time lag until the population no longer experiences any negative growth (in this case, for initial radii >= 3.8 and ε >= 0.036; for initial radii > 2.7, the rate of recovery slows slightly due to early growth followed by a transient decline that precedes ultimate recovery). When the initial population density varies (indicating the initial degree of maladaptation where a^2 = 0.3), (b) shows the rate of recovery with the initial radius fixed (as in Figure 5a where the radius = 1 and D/r = 1). In this case, extinction will occur without evolution not only for an initial density below the initial Allee threshold, but for any density since the initial radius is below the critical patch size. Hence, a non-zero rate implies evolutionary rescue and a zero rate means extinction.

(a)


Rate of Recovery (t^{-1})
0.4
0.3
0.2
0.1
0
0.1
0.08
0.06
0.04
0.02
0
Genetic Variance (ε)
1
2
3
4
Initial Radius

(b)


Rate of Recovery (t^{-1})
0.3
0.2
0.1
0
0.1
0.08
0.06
0.04
0.02
0
Genetic Variance (ε)
0.2
0.4
0.6
0.8
1
Initial
Population Density (u)

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CHAPTER 3

Allee effects, aggregation, and invasion success

Abstract

Understanding the factors that influence successful colonization can help inform ecological theory and aid in the management of invasive species. When founder populations are small, individual fitness may be negatively impacted by component Allee effects through positive density dependence (e.g., mate finding). Reproductive and survival mechanisms that suffer due to a shortage of conspecifics may scale up to be manifest in a decreased per-capita population growth rate (i.e., a demographic Allee effect). Phenomenological models based on mean-field assumptions and demographic Allee effects may not adequately capture how component Allee effects scale up when heterogeneous spatial structure influences conspecific availability. Thus, such models may mischaracterize the probability of establishment. In order to better assess how individual-level processes influence population establishment, we developed a spatially-explicit individual-based stochastic simulation of a small founder population. We found that increased aggregation significantly affects individual fitness and the population-level reproductive rate, a strong predictor of establishment probability. Since reproductive rate is sensitive to the scaling up of component Allee effects, details of dispersal and interaction kernels are important in scaling from individual parameters to population-level processes. Overall, we demonstrate the importance of considering both spatial

structure and individual-level traits in assessing the consequences of Allee effects in biological invasions.

Introduction

The seemingly distinct interests of conservation biologists and invasion ecologists converge on a common thread – understanding the factors that influence the viability of small populations. The ecological literature abounds with the broad notion that there is a positive relationship between population size and successful establishment and persistence (Lockwood et al. 2005). This relationship is due to demographic stochasticity, which has a stronger impact on smaller population sizes, but also reflects deterministic density dependence that increases the likelihood of extinction at low numbers. It has long been known that when a population is small, the reproduction and survival rates of individuals may decline with decreasing population density (Allee 1931), for a wide range of mechanistic reasons (listed in Holt et al. 2004). This principle has been empirically observed in numerous species ranging from bacteria to plants to animals. There is a growing recognition that such Allee effects can have profound consequences in natural populations and communities (Courchamp et al. 2008). With growing threats of species invasions, emerging infectious diseases and biotic homogenization, characterizing the factors that permit successful establishment at low numbers is challenging but essential.

In this paper we use an individual-based model to examine how different components of density dependence are experienced at the level of individuals, and how this translates into implications for population persistence of different density-dependent processes operating over different spatial scales. For positive density dependence to

occur in a population (what we call "demographic Allee effects"), it is necessary that a positive relationship exists between population size and at least one measurable component of individual fitness (what we call a "component Allee effect"). Conversely, however, net individual fitness may not be significantly depressed at low densities, despite the action of component Allee effects, if there is compensation in other fitness components that are enhanced at low density. An individual within a small population may be relieved of some density-dependent pressures (e.g., competition for resources), but is likely faced with others (e.g., finding a mate). The relative strengths of these processes may differ among otherwise identical individuals, due to their spatial position in the population and the spatial configuration of their neighbors. Conflicting demands on individuals can influence behavioral responses to such pressures. One strategy that might mitigate component Allee effects and thus affect population dynamics is limited dispersal leading to aggregation (Gascoigne et al. 2009). Essentially, the net effect of being in a small population may be different for each individual depending on its traits and its neighborhood, producing a range of ecological consequences, depending on how a population is spatially structured.

Models of population dynamics can either implicitly or explicitly make assumptions about how component Allee effects can lead to a demographic Allee effect (Taylor and Hastings 2005). Simple phenomenological deterministic models can easily describe population-level behavior through the use of a qualitatively sensible but ad hoc, bi-stable growth function representing demographic Allee effects. Such models, however, are not explicit in how component Allee effects can scale up to demographic Allee effects. Moreover, such models typically assume generalized mean field dynamics,

where each individual has an equal probability of interacting with every other individual. This assumption is unrealistic and may miss unexpected outcomes. One step towards incorporating spatially delimited interactions is to use spatial reaction-diffusion models (Chapter 2). Such models add a level of complexity to mean field approaches and can usefully address issues such as the asymptotic wave of advance of an invasion. For instance, Allee effects are expected to lead to critical spatial thresholds and slower rates of spread (Lewis and Kareiva 1993), arising due to dilution of local densities by dispersal (Taylor and Hastings 2005). However, reaction-diffusion models also leave out features of spatially localized movement and interactions that may be crucial for population persistence.

Population growth and spread are not only inherently spatial processes, but also include stochasticity. Random effects may lead to significant deviations from expectations from deterministic models, particularly when numbers are low, as in the initial phases of an invasion. Recognizing the importance of each individual being discrete and at a specific location in assessing population dynamics (Durrett and Levin 1994) ultimately implies that individual interactions should be explicitly addressed. Indeed, the inspiration for Allee effects originated from observations of interactions within animal aggregations (Allee 1931). We suggest that the detailed spatial patterning of individuals across a landscape can influence the magnitude of component Allee effects and ultimately influence persistence and invasion dynamics. Individual behavior and demographic rates should be primarily impacted by the local environment in which an individual resides, including individuals with whom it interacts. Thus, characterizing the spatial structuring of local neighborhoods should be particularly important in scaling up

to population-wide density dependence in births and deaths. A detailed portrayal of intraspecific interactions and individual behaviors in a spatially-explicit context is, we argue, essential to understanding emergent characteristics of successful establishment and spread.

To investigate if (and how) component Allee effects scale up to demographic Allee effects, and to disentangle the influences of spatial structure, dispersal, and local interactions on population dynamics, we developed a spatially-explicit individual-based stochastic simulation of an invasion process for a small founder population with localized interactions. Our results help explain how even very small populations can sometimes establish, despite the existence of overall strong positive density dependence leading to Allee effects and the expectation of heightened extinction risks at low numbers (Courchamp et al. 2008; Gascoigne et al. 2009). Our primary aim is to develop a deeper understanding of the ecological consequences of Allee effects and how small founder populations could succeed – despite processes leading to strong positive density dependence, that on the face of things would seem to doom them to extinction.

Individual-Based Model (IBM)

Because invasions are inherently stochastic spatial processes, we constructed the IBM to incorporate randomness in birth, death and movement events, in continuous space and time. We formulated a stochastic version of a well-studied, reaction-diffusion model (Lewis and Kareiva 1993; Murray 1993; Keitt et al 2001; Kot 2001; Drake et al 2005; Drury et al 2007; Chapter 2) to ensure that we adequately captured the dynamics of population growth and spread with density dependence. In this deterministic model, shown as follows,

$$\frac{\partial N(x,t)}{\partial t} = rN(x,t)\left(\frac{N(x,t)}{a} - 1\right)\left(1 - \frac{N(x,t)}{K}\right) + D\nabla^2 N(x,t)\,, \qquad (1)$$

$N(x,t)$ is population size, which is a function of position, x, and time, t. The population growth rate depends on the intrinsic growth rate r (assumed positive), as well as the population size relative to both an Allee threshold, a, and an environmental carrying capacity, K, where $0 < a < K$. If the population is below the Allee threshold, it has negative population growth and faces certain extinction. Thus, the Allee threshold represents the minimal population size for population survival; the carrying capacity represents maximal population size if invasion succeeds. The diffusion coefficient, D, scales the rate of population spread across a one- or two-dimensional habitat. Given diffusion with an Allee effect, the initial population for model (1) must be large enough over a sufficiently large initial area in order to survive (Lewis and Kareiva 1993; Murray 1993; Kot 2001; Drake et al. 2005; Drury et al. 2007; Chapter 2).

Using this population model as the basis for our stochastic individual-based simulation, we interpreted eqn. (1) from an individual perspective and defined birth, death and movement events accordingly. The simulation is an event-driven Markov process based on the Gillespie algorithm with inter-event times exponentially distributed (Gillespie 1977; Renshaw 1991; Birch and Young 2006; Erban et al. 2007). This framework allows birth and death events to occur in continuous time, where individual i has a birth rate, b_i (the rate at which the individual gives birth) and death rate, d_i, each of which depends on the local density, N_i. A neighbor-counting scheme is used to find the local density N_i (population within individual i's neighborhood), given a particular local interaction kernel (i.e., the distance-dependent interaction between a given individual and

its neighbors). For the top-hat interaction kernel (Figure 1A), for instance, N_i is the sum of the number of individuals within a specified distance, S_T, from individual i.

The relations used for birth and death rates are

$$b_i = \frac{N_i}{a} + \frac{N_i}{K} = \frac{N_i(a+K)}{aK}, \quad d_i = 1 + \frac{N_i^2}{aK} = \frac{aK+N_i^2}{aK} \tag{2}$$

(similar to those in Ackleh et al. 2007). When the local density $N_i = a$ or K, birth and death rates are equal and the growth rate is 0. For N_i between these values, the birth rate exceeds the death rate and the growth rate is positive, while outside these values the death rate is higher than the birth rate. Therefore, a describes an Allee threshold and K a carrying capacity. Births and deaths are assumed to be independent Poisson processes. This means that the birth rates and death rates of all individuals can be summed to give an overall event rate E for the population. Since the sum of Poisson processes is also a Poisson process, at any time the time until the next event (birth or death) is exponentially distributed with a mean of $1/E$.

Once the simulation is initialized with the starting individuals, birth and death rates are calculated for each individual. These are summed to give the initial E. A random deviate with an exponential distribution with mean $1/E$ is then generated. This gives the time until the first event, and time is advanced by this amount. This first event could be either death or reproduction of any individual. The probability that it is the death of individual i is d_i / E, and the probability that it is its reproduction is b_i / E. A uniform random deviate is used to assign the event to the proper individual. If the event is a death, the individual is deleted; if it is reproduction, a new individual is added to the population at the parental location. Next, the position of each individual is adjusted (see below), its birth and death rates calculated for the new local density, and the event rates

summed to give the new E. The time until the next event is generated, time is advanced by this amount, and the event is assigned to an individual, as before. This process is then repeated for the duration of the simulation.

The simulation follows a population of discrete organisms of a single species introduced into a two-dimensional landscape. The spatial framework consists of a physically homogeneous environment treated as a continuous region (as opposed to a discrete lattice), assumed large enough (in our simulations 1000 x 1000) for edge effects to be negligible and with periodic boundaries. An individual i is located at coordinates (x_i, y_i), and every individual, including newborns, moves following any birth or death event that occurs anywhere in the population, in order to approximate continuous rates of movement. In order to closely approximate Brownian motion (i.e., the second term in eqn. (1) which is the diffusion component), the distance an individual moves is normally distributed with mean 0 and variance $2D\Delta t$ (Birch and Young 2006; Twomey 2007). Δt is the time since the last event and is generally sufficiently small to adequately approximate continuous movement. The direction moved is random, with all directions equally likely. Individual i's new coordinates after this bout of movement are given by:

$$x_i(t + \Delta t) = x_i(t) + \sqrt{2D\Delta t}\,\xi_x, \;\; y_i(t + \Delta t) = y_i(t) + \sqrt{2D\Delta t}\,\xi_y \qquad (3)$$

where, ξ_x and ξ_y are independent zero-mean unit-variance Gaussian random deviates. (These are generated using $\xi_x = \sqrt{-2\ln U}\cos 2\pi\theta$, $\xi_y = \sqrt{-2\ln U}\sin 2\pi\theta$, where U and θ are uniform random variables in the interval [0,1)).

The top-hat interaction kernel, with finite boundaries, represents, in a sense, a restricted spatial scale within which individuals perceive their local density, and outside of which they do not (i.e., they are short-sighted in sensing conspecific neighbors). We

also implemented two other local interaction kernels (for individuals to count neighbors, N_i, influencing the extent of experienced density-dependence). These were a bivariate Gaussian function, $N_i = \sum_j M \exp\left(-(d_{ij})^2/2{S_M}^2\right)$, and a Laplace or back-to-back exponential distribution, $N_i = \sum_j W \exp\left(-S_W(d_{ij})\right)$ (Figure 1B and C, respectively). In these cases, S_M and S_W determined the width of the kernels and *M* and *W* are scalars that influence the weight that each individual *j* places on individual *i* as a determinant of its fitness components, given their Euclidean distance apart, d_{ij}. These parameter values (Table 1) were assigned in order to maintain consistency and to generate results broadly comparable across kernels, given similar initial conditions. Because the impact of the spatial scales of density-dependence and dispersal have to be assessed relative to each other (Murrell 2006), we present our results with fixed widths for the local interaction kernels, while varying dispersal rates over the range that was found to produce any possibility of successful establishment.

The distance, d_{ij}, between individuals influences reproduction and survival because the strength of component Allee effects are based on local density, where what counts as 'local' for an individual is determined by the interaction kernel. In order to track distances between individuals and better gauge how their spatial distribution and degree of clustering influence individual- and population-level behavior, we use Ripley's K statistic, a second-order spatial point pattern analysis technique that measures deviations from spatial homogeneity (Ripley 1976). Ripley's K is defined as

$$\widehat{K}(R) = \lambda^{-1} \sum_i \sum_{j \neq i} I(d_{ij} < R)/N \quad (4)$$

where *N* is the total number of individuals, λ their density (number of individuals divided by the total occupied area), and d_{ij} the Euclidean distance between individuals *i*

and j. I is an indicator function that equals 1 if the distance between individuals is less than R and 0, otherwise. In other words, $\widehat{K}(R)$ is the cumulative tally of the proportion of all individuals separated by distances less than R (Fortin and Dale 2005). In these calculations, the total occupied area is the area of a circle encompassing the entire population, with the radius the distance from the center of the plot to the farthest individual. Sometimes a buffer zone is used in calculating Ripley's K (Hasse 1995). However, given our protocols and the goal of comparing Ripley's K statistics in a relative context, the addition of a buffer zone (Haase 1995) as an edge correction factor would not have contributed any new information. The overall interpretation of this metric in the context of the following simulations is that it describes relative clustering. For example, if the individuals are over-dispersed, $\widehat{K}(R)$ will be small, but will take on larger values with more spatial structure and clustering for a fixed R (Fortin and Dale 2005).

For direct comparisons of the effects of spatial structure, dispersal rate (D), and local interaction kernel on individual behavior and population dynamics, certain parameter values and initial conditions were maintained across simulations (i.e., initial population size, maximum area of initial introductions, Allee threshold a, and carrying capacity K), while other parameter combinations were varied (see Table 1). Specifically, each simulation was initialized with 25 individuals randomly distributed across a unit circle at the center of the plot, and the Ripley's K statistic (for $R = 1$) describing the initial spatial distribution was recorded. These initial conditions were chosen such that each introduced population was at the tipping point (Allee threshold) of critical size and area based on the analytically derived conditions of the deterministic demographic Allee effect model (Chapter 2). Due to the stochastic nature of this model, we simulated 100

replicates for each combination of initial Ripley's K from 1.2 to 2.5 by intervals of 0.1, and dispersal rate, from 0.001 to 0.100 by 0.001, for a total of 140,000 runs for each local interaction kernel. Simulations were run until the population either went extinct or at least a total of 100 time units had elapsed.

In order to focus on the relationship between an individual's extrinsic environment (local density) and the intrinsic density-dependent birth-death process, rather than other kinds of heterogeneity among individuals, we fixed a and K to be the same for each individual. Fixing parameters in this way allows us to test how identical individuals faced with different circumstances elucidate the interaction between component Allee effects (i.e., the strength of Allee effects, which is also affected by the carrying capacity or negative density-dependent effects) and an individual's biotic environment (i.e., the spatial structure of conspecifics) by treating individual fitness (i.e., r_i, the difference between birth and death rates) as a proxy for this interaction. Given that every population is introduced into a similar context with individuals that are not intrinsically different, we can determine how and why endogenous spatial heterogeneity becomes an important factor in the probability of establishment and persistence.

Results

We observed the emergence of departures from population-level, mean field behavior (especially with non-spatial models) when the strength of component Allee effects interacts with spatial structure and affects individual fitness. The outcome of this interaction is well illustrated by comparing Figures 2A and B, which show two populations of identical invaders ($D = 0.05$) with differing initial spatial structure. Initially, from the global perspective, the overall density is the same ($\lambda = 7.96$, 25

individuals in a circle of area π). From the individual perspective, however, the local density differs as indicated by the Ripley's K statistic (at $t = 0$, Ripley's K for Figure 2A is 1.6 and Figure 2B is 2.4). The subsequent snapshots through time reveal that when the initial population is small, the population with the more clumped initial distribution (Figure 2B) succeeds in establishing. This is because higher average local densities have more births than deaths (at least in some regions). The population with the less clumped initial distribution (Figure 2A), with lower local densities, by contrast declines due to the Allee effect. Aggregation thus can minimize the negative impacts of Allee effects.

Figures 3A and B, on the other hand, show populations introduced with equivalent spatial structures (i.e., Ripley's K = 2.0), but different dispersal ability (D = 0.001 for Figure 3A and $D = 0.1$ for Figure 3B). Increased dispersal rates destroy the spatial structure (i.e., Ripley's K decreases over time), and the population inexorably goes extinct. Where individuals remain in close proximity to each other, because they are sluggish dispersers, they can mitigate component Allee effects and thus successfully establish. The clumped distribution that influences this result emerges from constrained short-distance dispersal and is enhanced as more offspring are produced and remain within clusters.

To further demonstrate this point, Figure 4 illustrates the effect of dispersal rate on spatial structure over time. These simulations were all initialized with a similar spatial structure value describing their initial spatial distribution (i.e., Ripley's K = 2.0) and dispersal rate was varied. Out of 200 replicates for each dispersal rate, each trajectory represents the average Ripley's K over time, grouped by whether or not the population went extinct. It should be noted that the proportion of extinctions increased from

approximately 60% to 90% as the dispersal rate increased from 0.001 to 0.10. Although increased dispersal reduces the spatial structure, the population can succeed by chance, however not as readily as one that maintains a higher degree of clustering. Likewise, even though reduced dispersal helps retain spatial structure, establishment is not guaranteed: the population (due to other sources of stochasticity) can easily fail to establish.

Overall, in drawing the connection between individual fitness and demographic Allee effects, we have presented the impact of spatial structure on individual fitness as a modulator of the probability of population success. Figure 1 demonstrates this by showing that spatial structure influenced by dispersal rate interacts with component Allee effects and scales up to impact population persistence. The probability of invasion success (denoted by the colorbar on the side of Figure 1F) is calculated as the proportion of the 100 replicates for each parameter combination (Ripley's K and dispersal rate) that show an increase in population size after a total time of 100 time units [i.e., $N(t = 100) > N(t = 0)$]. Despite the odds being against successful establishment (with only 25 individuals initially introduced), the probability of invasion success is highest with high spatial clustering and short-range dispersal (top left corner) and lowest with over-dispersion and a high dispersal rate (bottom right corner). This is further evident with probability density plots of initial individual fitness r_i (Figure 1G, H, and I) across 100 replicates for each parameter combination, indicated by the placement of the letters a-c in the corresponding probability of invasion success plot. It is clear that the probability of establishment decreases from top left to bottom right, primarily because initial individual fitness is generally negative (i.e., death rates outweigh birth rates) unless there is

sufficient spatial structure. As the initial spatial structure is reduced, mean individual fitness decreases, while the skewness of the distribution shifts from negative to positive.

Durrett and Levin (1994) claimed that "one should not worry too much about what neighborhood to choose [since] in most cases, qualitative behavior of the model does not depend on the neighborhood used." Our results in Figure 1D, E, and F are consistent with this perspective. We found that spatial structure becomes less important as the local interaction kernel is varied from top-hat to normal to exponential, but the population dynamics are qualitatively similar for the different kernels. This is shown across Figure 1, as the contour plot shifts with the particular kernels opening up a larger range of parameter space that lead to higher probabilities of success. As individuals can detect farther neighbors, beyond the restricted spatial scale of the top-hat perspective, through fatter tailed kernels, local spatial structure matters less and less, component Allee effects merge into demographic Allee effects and departures from mean-field predictions are not as striking.

Discussion

To investigate how spatial structure interacts with component Allee effects and scales up to impact demographic rates, we considered the importance of spatial structure from the individual point of view. We constructed a population model by summing over spatially shifting effects experienced at the level of individuals. The way in which a population is clustered proves to be of key importance in relaxing the potentially negative impacts of Allee effects on population persistence. We observed interesting departures from deterministic reaction-diffusion models, where some populations either depended on a clustered initial spatial distribution or tended to develop strong spatial clustering in

order to successfully establish and avoid extinction. This phenomenon occurred because with clustering and limited dispersal individuals were able to mitigate component Allee effects based on their local, as opposed to global, density.

We observed that local interactions play a significant role in the successful establishment of a population. Because the density of conspecifics within an individual's interaction neighborhood, based on the spatial structure of the population, impacts individual fitness (i.e., birth and death rates), the initial spatial distribution upon introduction is a key determinant of successful establishment. We further demonstrated that the dispersal rate strongly influences the spatial structure over time and hence becomes an additional important factor in affecting establishment as well as future invasion dynamics. High dispersal tends to move individuals away from temporary clusters, aggravating the demographic costs represented in component Allee effects. Based on these characteristics, we illustrated a range of scenarios where component Allee effects may either be suppressed (where the population succeeds in establishment) or result in depressed demographic growth rates leading to extinction. There is thus a crucial feedback between the spatial pattern of individuals across the landscape, and the emergent dynamics of the population (Durrett and Levin 1994; Bolker and Pacala 1997).

This feedback has previously been recognized in terms of trade-offs between growth and spread for survival of a population in a patchy habitat (Skellam 1951; Kierstead and Slobodkin 1953; Okubo 1980; Murray 1993). The idea was originally couched in terms of phytoplankton blooms that arise when a critical area is occupied such that the population avoids extinction by overcoming the dilution effect (i.e., where sufficient reproduction compensates for the loss due to diffusion; Skellam 1951;

Kierstead and Slobodkin 1953; Okubo 1980). By shifting the focus from the exogenous environment (and discrete patches of differing quality), Allee effects in effect generate this same dynamic, constraining further range expansion at the periphery when populations are too small, are too short lived, or produce too few propagules because of reduced net reproduction (Hengeveld and Hemerik 2002). This is a fundamental ecological and spatial consequence of Allee effects (i.e., an invasion front that is a result of being "pushed" from the inside out, as opposed to being "pulled" by the leading edge; Lewis and Kareiva 1993; Keitt et al 2001; Chapter 2). This basic concept is revealed in our simulations where, due to the apparent breakdown of spatial structure by long distance dispersers, individual fitness is depressed, scaling up to generate population decline.

Our investigation has focused on the early stages of invasion (i.e., introduction and establishment; Williamson 1996). However, spatially constrained dispersal and interactions can also influence long term dynamics. As limited dispersal allows individuals to overcome component Allee effects, a trade-off between positive and negative density-dependence emerges when the population grows close to carrying capacity for a given cluster of individuals. We have observed patterns shaped by competition where clusters at carrying capacity are separated far enough to reduce interaction (similar to patterns reported by Birch and Young 2006). Since we have shown that constraints on dispersal rate are needed for successful establishment, it is likely that consequently population growth and invasion speed will be slower overall in populations with Allee effects following the initial transient phase of establishment (Shigesada and Kawasaki 1997; Johnson et al 2006; Murrell 2006; Tobin et al 2007). In

this sense, our model accords with previous studies that have explored spread dynamics in other contexts, and this body of literature collectively shows that the Allee effect gives rise to range pinning and patchy invasions, pulsed range expansion, and overall slower rates of spread (see Taylor and Hastings 2005 for a review).

The existence of spatial patterns as a consequence of Allee effects has been recognized empirically in a number of different taxa (Taylor and Hastings 2005; Courchamp et al. 2008). For example, the invasion of the gypsy moth across the U.S. proceeded in a series of temporal pulses, due to strong mate-finding Allee effects requiring high density prior to spread (Johnson et al. 2006). Interestingly, the Allee threshold has been shown to differ depending on the environment (akin in our models to varying the strength of the component Allee effect within an individual's local neighborhood), due to the effectiveness of pheromone transmission, and hence Allee effects have slowed invasion speed or even reversed the invasion, forcing range contraction in certain locations (Tobin et al. 2007). Generally, in species where density can be critical to fertilization efficiency, aggregations can enhance survival through environmental conditioning, predator dilution, anti-predator behavior and increased foraging efficiency (Stephens and Sutherland 1999; Berec et al. 2007; Courchamp et al. 2008; and references therein). It is likely that component Allee effects influence individual fitness, but whether or not demographic Allee effects are thereby present and population dynamics are affected depends on local intraspecific interactions as modulated by dispersal and the spatial scale of the interactions. Because the strength of component Allee effects may vary in time and space (due in part to indirect effects), their presence

does not always imply demographic Allee effects (Courchamp et al. 2008; Gascoigne et al. 2009).

In the general context of biological invasions, spatial dynamics are important across multiple levels of organization (see Lion and van Baalen 2008 for a review). The impact of local interactions and spatial dynamics are also similarly related in understanding the outcome of interspecific interactions, such as interspecific competition (Gandhi et al. 1998, 1999; Korniss and Caraco 2005; Allstadt et al. 2007) and consumer-resource, predator-prey, or pathogen-host systems (Tilman and Kareiva 1997; Dieckmann et al. 2000). Our model adds to these studies, by highlighting the importance of a particular class of intraspecific interactions. Our model incorporates positive density dependence at low densities and focuses on how component Allee effects are mitigated due to spatial structure and low dispersal in the early phases of invasion, and so we in effect have emphasized the benefits of aggregation in the intraspecific context. We hypothesize that this context may give rise to selection for reduced dispersal since long distance dispersal would likely be suicidal when the population is small (Gyllenberg et al 2002; Parvinen 2004); any individual who goes a long distance from a transient cluster is likely to find itself alone, where it loses the fitness advantages accruing from proximity to conspecifics. Presently, our model intentionally overlooks evolutionary consequences of Allee effects (Wells et al. 1998; Holt et al. 2004; Courchamp et al. 2008; Gascoigne et al. 2009; Chapter 2) and other behavioral responses (e.g., complex movement rules and density-dependent dispersal; Etienne et al. 2002; Morrell and James 2008), in order to thoroughly understand the ecological consequences of Allee effects, and to characterize how local processes translate into global dynamics. Clearly, a next step in understanding

the full implications of Allee effects is to incorporate adaptive evolutionary processes and relevant behavioral responses in order to investigate how the limited dispersal we suggest may at times be absolutely required for initial establishment could nonetheless evolve into greater dispersal rates, hypothesized to occur as evolution occurs during invasion into new landscapes.

Table 1

Parameters , their descriptions and values used		
Parameters	Meaning	Range
a	Allee threshold	25
K	Carrying capacity	100
D	Dispersal distance	0.001-0.100
S_T	Width of Top-hat kernel	1.0
M	Scalar for Gaussian kernel	1.25
S_M	Width of Gaussian kernel	1.0
W	Scalar for Laplace kernel	1.85
S_W	Width of Laplace kernel	1.0
R	Distance for Ripley's K statistic	1.0
$\widehat{K}_0(R)$	Ripley's K for initial spatial distribution	1.2-2.5

Figure 1: The effect of initial spatial structure (Ripley's K) and dispersal rate (*D*) on individual fitness and overall invasion success of a population. Top-hat (A), Gaussian (B), or Laplace (C) indicate the local interaction kernel that was used to generate the results in each column, respectively. The probability of invasion success (D,E,F) (white indicates values > 30%) is calculated as the proportion of 100 replicates that show an increase in population size by the end of the simulation. The density subplots (G,H,I) correspond to the parameter combinations indicated by the letters (a-c) in the probability plot and show the relative frequencies of individual fitness (r_i) at time of introduction (t=0).

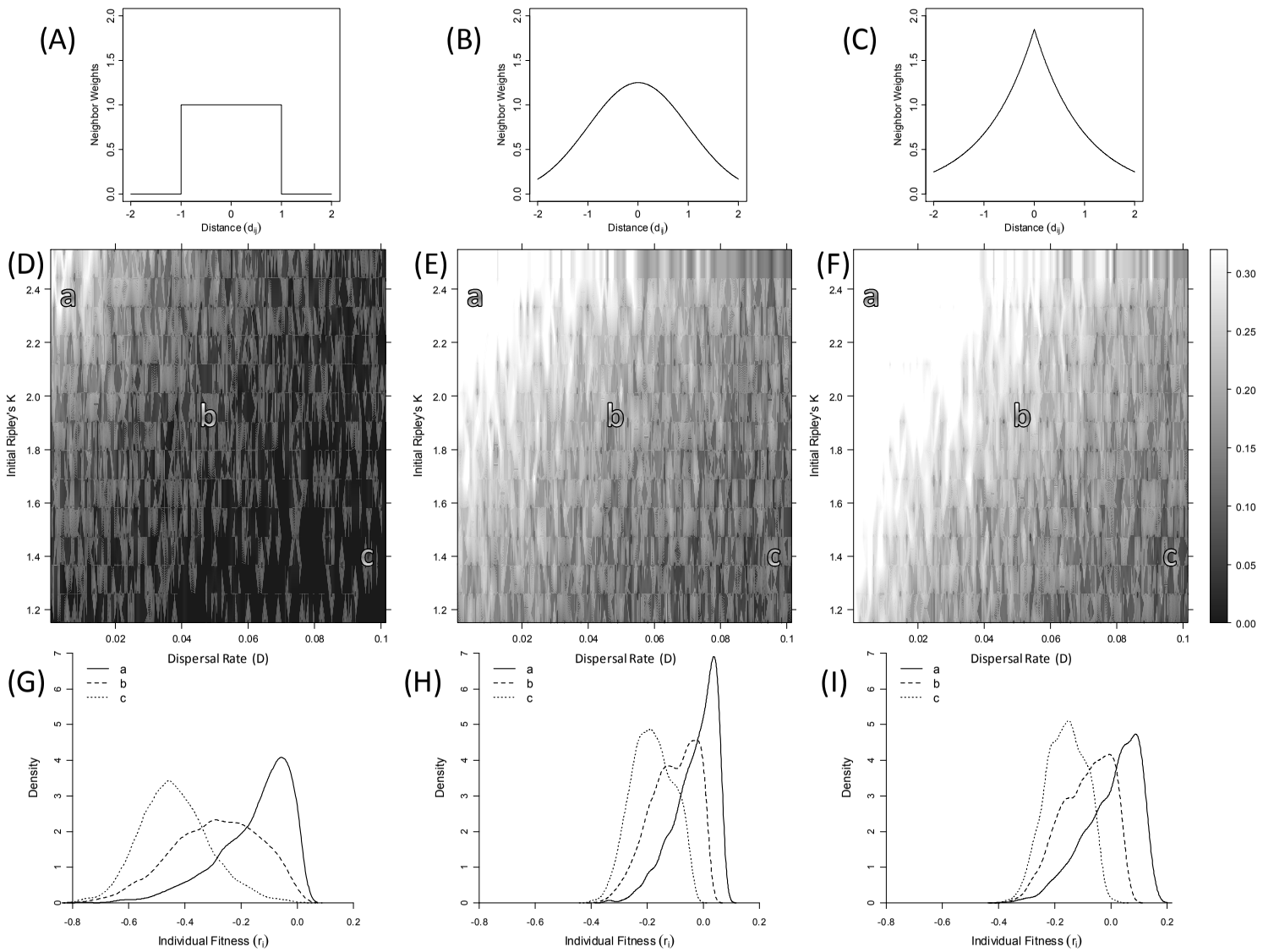
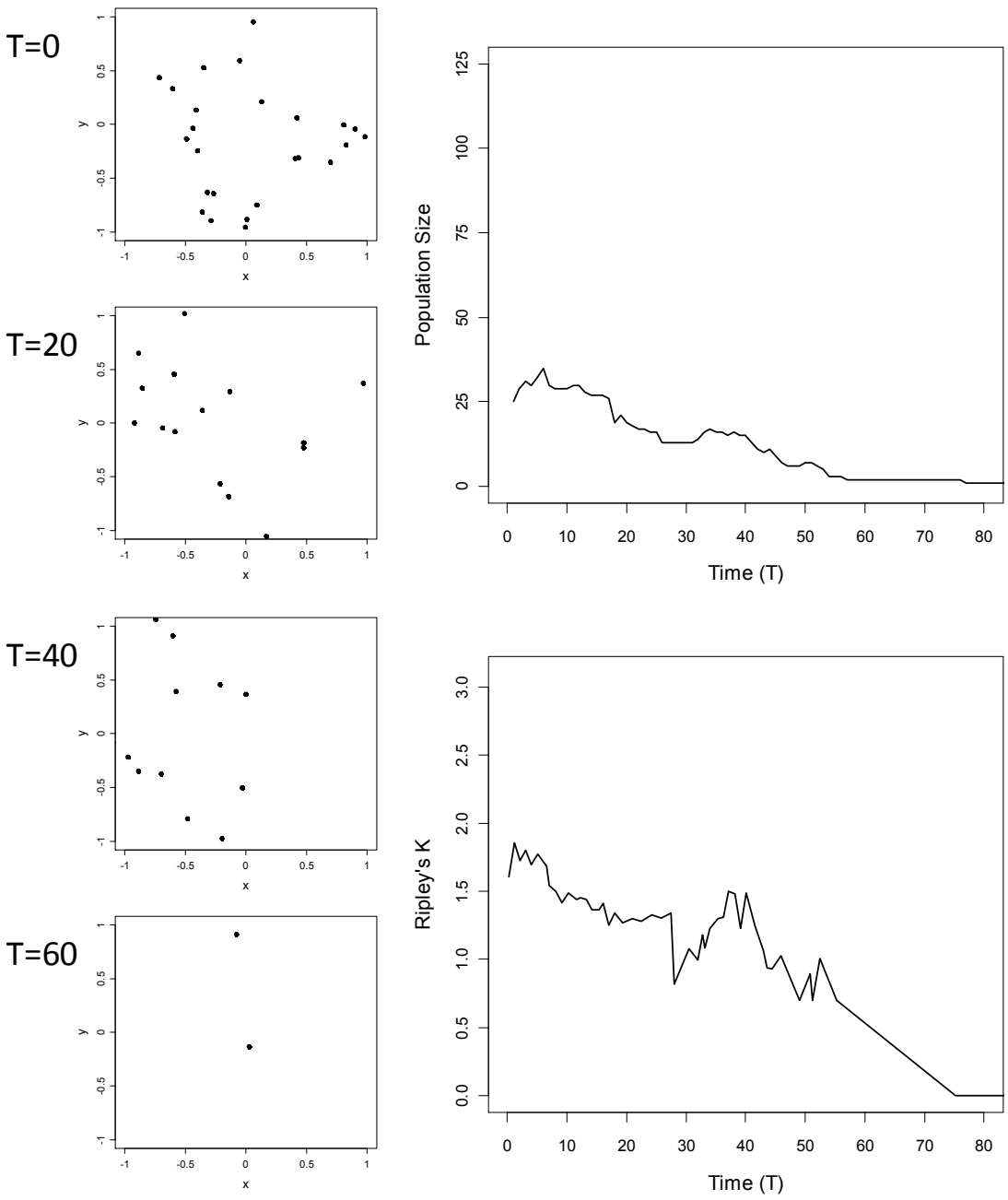

(A)
(B)
(C)
Neighbor Weights
Distance (d_{ij})
(D)
(E)
(F)
a
b
c
Initial Ripley's K
Dispersal Rate (D)
(G)
(H)
(I)
Density
Individual Fitness (r_i)

Figure 2: Realizations of simulations of populations where individuals are identical except for initial spatial structure. In each case, temporal snapshots show how individuals are distributed across space following the introduction of 25 individuals within a unit circle. The corresponding graphs show the temporal dynamics describing how population size and spatial structure (Ripley's K) change. In (A), the dispersal rate is the same as in (B), where $D = 0.05$; however, individuals are initially over-dispersed in (A) with Ripley's K = 1.6, and this loosely structured population declines steadily to extinction. Individuals in (B), on the other hand, are tightly clumped initially, with Ripley's K = 2.4, and maintains this level of aggregation until the population successfully grows. The top-hat local interaction kernel was used and other parameter values are given in Table 1.

(A)



(B)

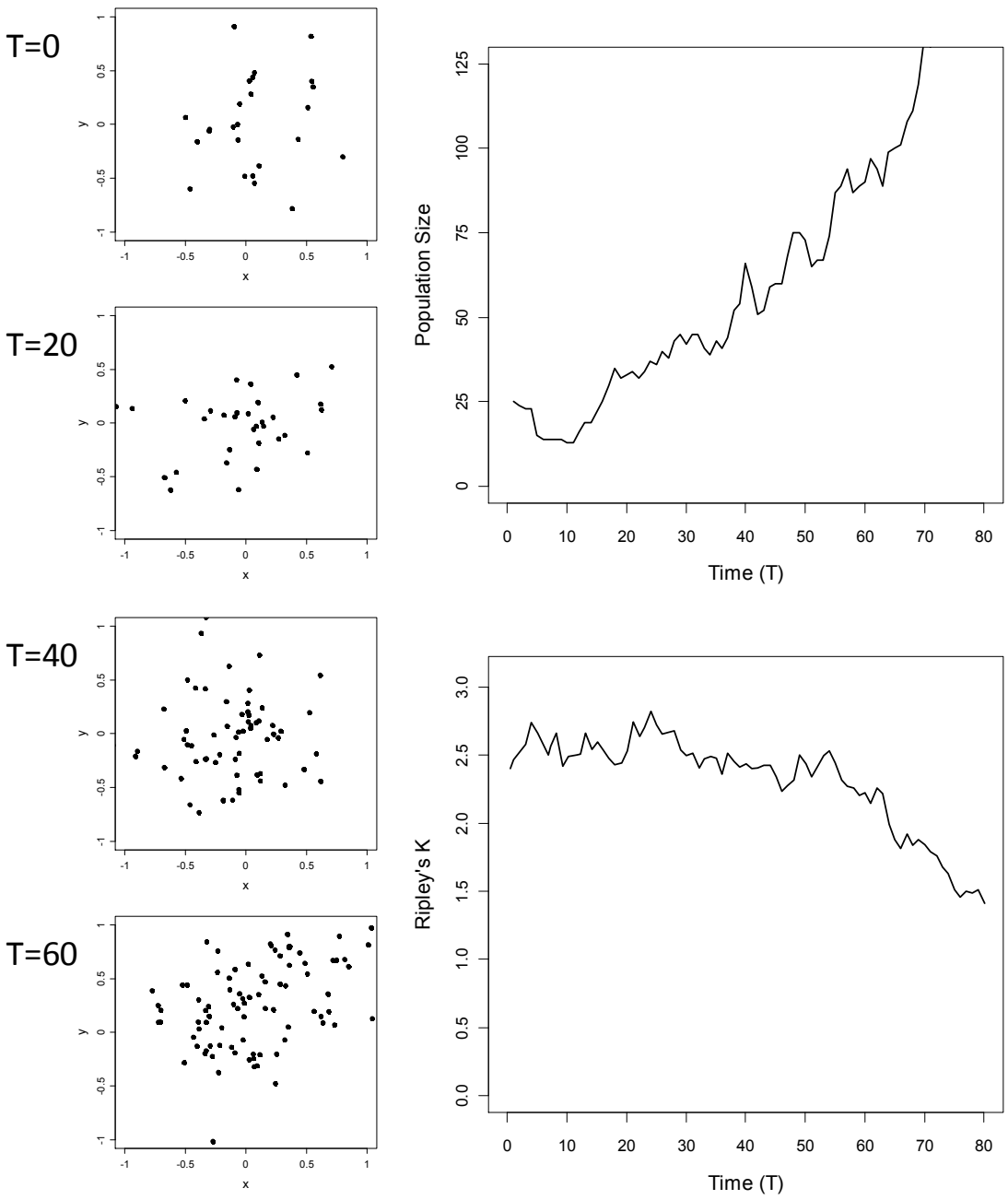
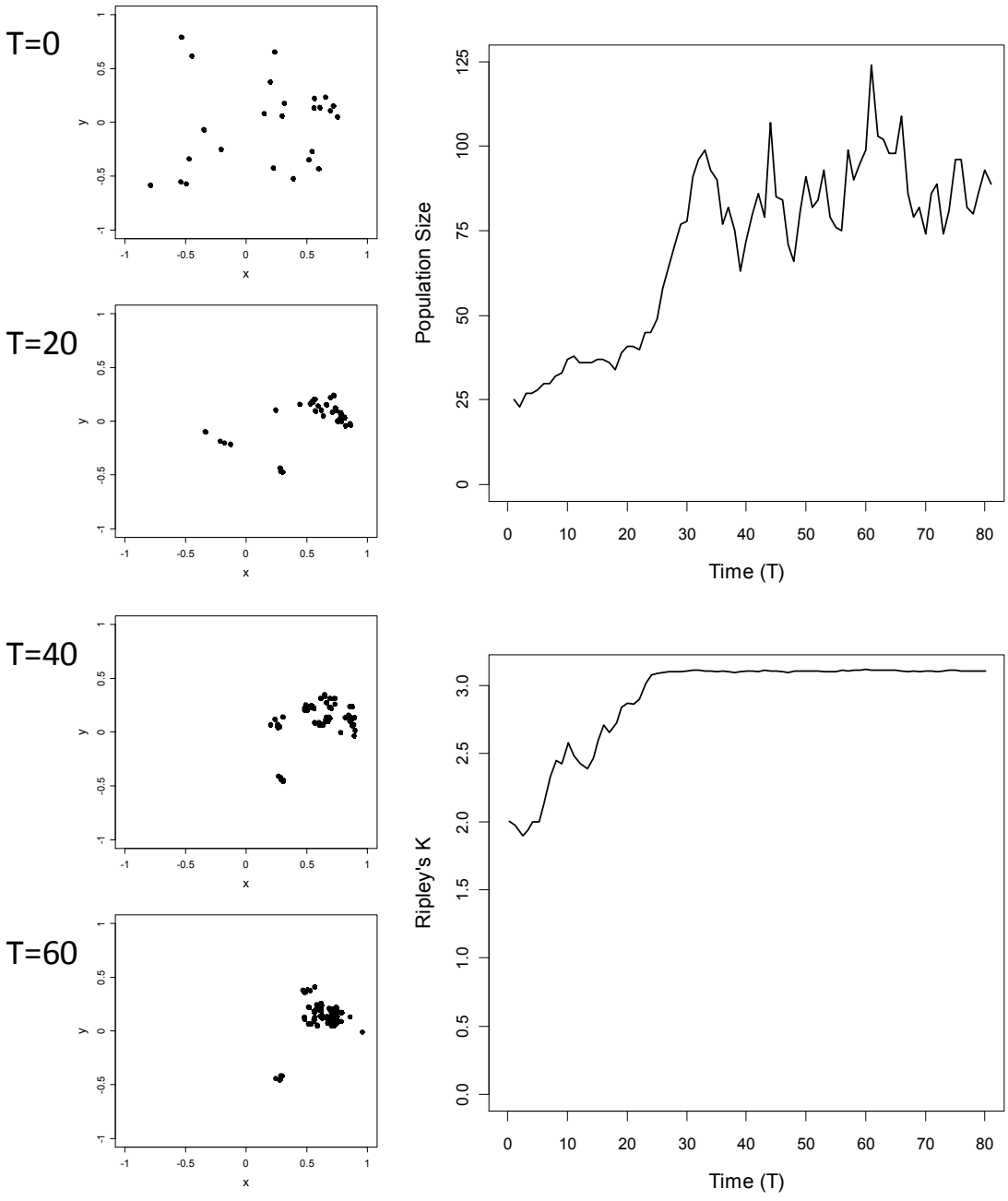


Figure 3: Realizations of simulations of populations where individuals are identical except for dispersal rate. In each case, temporal snapshots show how individuals are distributed across space following the introduction of 25 individuals within a unit circle. The corresponding graphs show the temporal dynamics describing how population size and spatial structure (Ripley's K) change. (A) and (B) are instances where individuals have identical initial spatial structure (Ripley's K = 2.0), but differ in dispersal ability with $D = 0.001$ and 0.1, respectively. In these cases, short range dispersal in (A) leads to spatial aggregation and population growth, whereas long distance dispersal in (B) destroys spatial structure and proves suicidal for individuals. The top-hat local interaction kernel was used; other parameter values are given in Table 1.

(A)



(B)

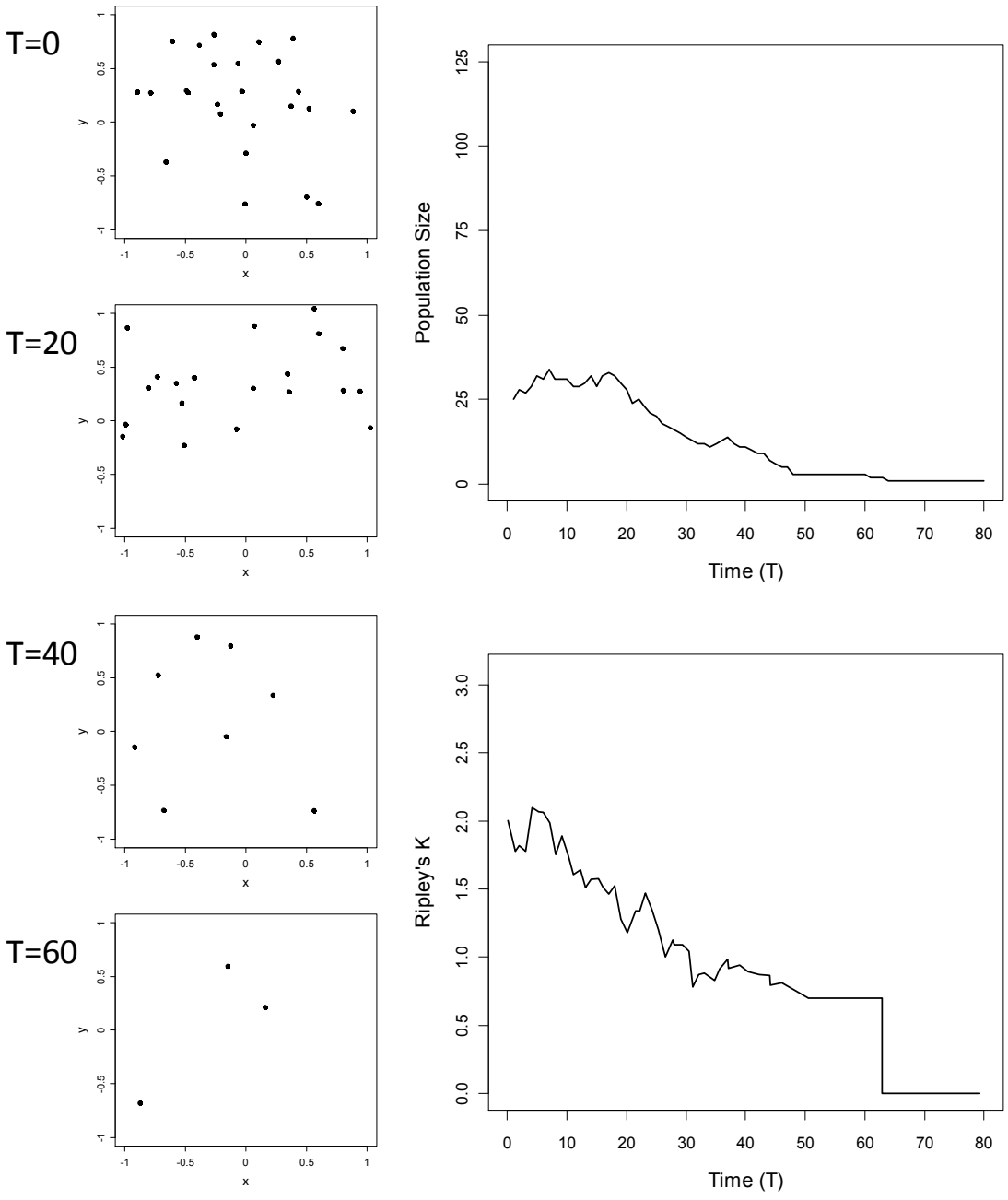
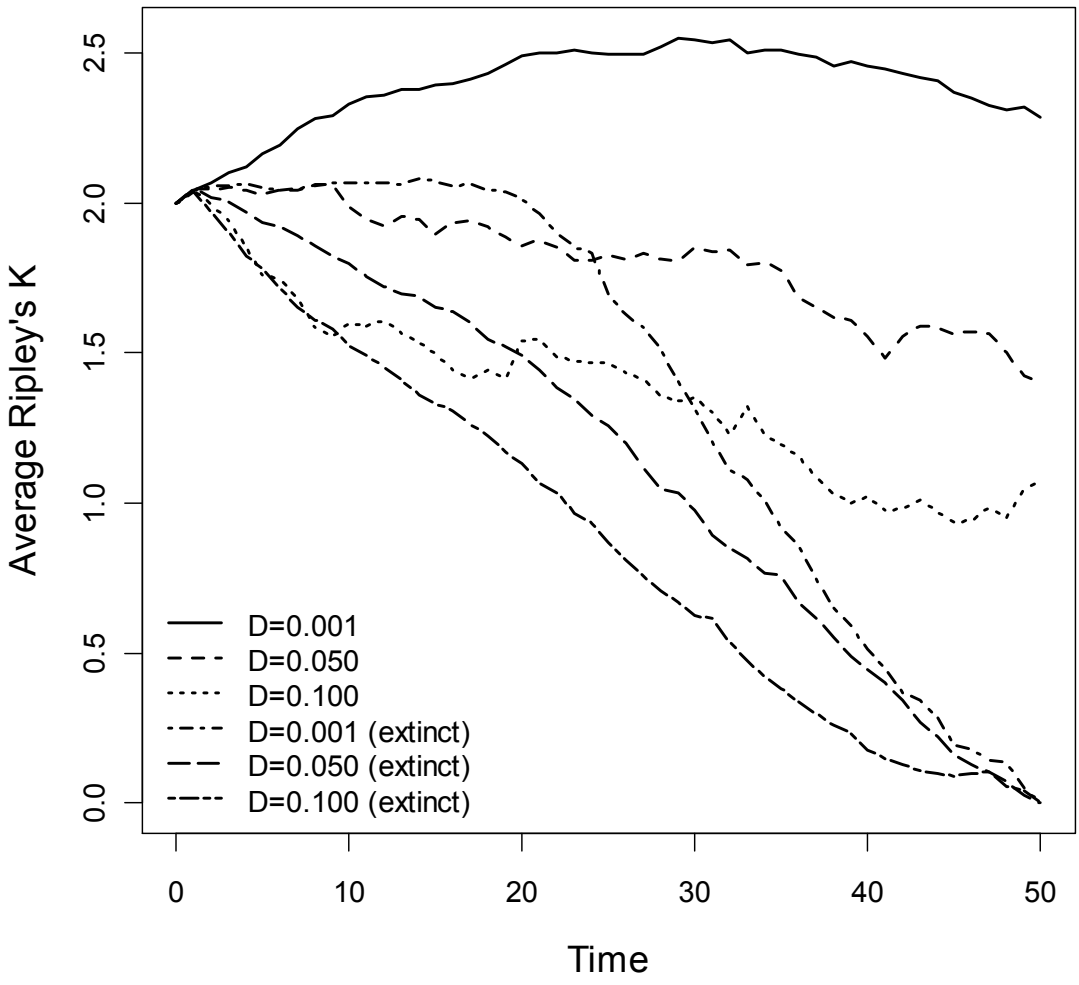


Figure 4: The effect of dispersal rate (*D*) on spatial structure (Ripley's K) over time. Each replicate simulation was initialized with similar spatial structure (Ripley's K = 2.0), while dispersal rate was varied from short (*D* = 0.001) to intermediate (*D* = 0.05) to long (*D* = 0.1). Average Ripley's K values over 200 replicates for each dispersal rate are grouped by whether the population went extinct or succeeded. 40% succeeded for *D* = 0.001, 20% succeeded for *D* = 0.05, and 10% succeeded for *D* = 0.1.



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CHAPTER 4

Overcoming Allee effects through evolutionary, genetic, and demographic rescue

Abstract

Studies of biological invasions frequently acknowledge a phenomenological paradox wherein despite the amplified threats of extinction facing small founder populations, successful colonization occurs nonetheless, bringing devastating ecological and economic consequences. We addressed this paradox by exploring the importance of evolutionary processes given the time constraints generated by ecological factors driving the population to extinction. When a population is introduced at low density, individuals often experience a reduction in one or more components of fitness due to novel selection pressures that arise from diminished intraspecific interactions and positive density dependence (i.e., component Allee effects). Although the time to extinction may be limited, there is a chance that the population can adapt and recover on its own (i.e., evolutionary rescue) or through additional immigration contributing to the population size (i.e., demographic rescue) and/or enhancing the genetic variation (i.e., genetic rescue). Within a spatially-explicit modeling framework, we consider the relative impact of each type of rescue on probability of success by following the evolution of a multi-locus quantitative trait that influences the strength of component Allee effects. We demonstrate that because the ecological system is significantly density driven, the effect of demographic rescue provides the greatest opportunity for success. While highlighting

the role of evolution in the invasion process we underscore the importance of the ecological context influencing the persistence of small founder populations.

Introduction

A fundamental question for the preservation of biodiversity and ecosystem health is, "what minimal numbers are necessary if a species is to maintain itself in nature?" (Allee 1938). The balance between extinction and persistence relies heavily on the circumstances faced by small populations and affects both endangered and invasive species. It is generally recognized that the more individuals there are in a population, the less likely it is to become extinct (Lockwood et al. 2007). Maintaining a sufficient population size acts as a buffer from positive density dependence (i.e., Allee effects), demographic and environmental stochasticity, and may provide the opportunity for adaptive response to novel selection pressures (Lande 1988). During the introduction phase of biological invasions, populations may be reduced to such low density that they experience an extremely high risk of extinction. However, if demographic constraints and stochastic effects are not too severe, the population can persist long enough to adapt and recover (i.e., evolutionary rescue; Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007; Chapter 2), or be rescued by additional immigrants (Brown and Kodric-Brown 1977). The influx of immigrants can significantly impact population viability by simply increasing the population size thereby reducing the demographic threats of extinction (i.e., demographic rescue), and/or introducing genetic variation that increases (i.e., genetic rescue) or decreases mean fitness (Sakai et al 2001; Holt et al 2004; Tallmon et al 2004; Garant et al 2007). These various forms of rescue have often been invoked as possible explanations for specific invasions (Simberloff 2009), but their relative

importance to invasion more generally is not understood. Since the success of a small population is determined by the interplay between ecological and evolutionary processes that influence the time to extinction, it is essential to disentangle the effects that evolutionary, demographic, and genetic rescue have on that dynamic feedback relationship in order to understand more generally how rescue impacts invasion.

Intraspecific interactions are a primary factor influencing the relationship between these ecological and evolutionary processes, especially for sexually reproducing species. The ability to find a mate and reproduce increases the population size and generates new types that enhance genetic variation and hence evolutionary potential. Other intraspecific interactions play similar roles by enhancing survival through environmental conditioning, predator dilution, anti-predator behavior, foraging efficiency, and other effects (Stephens and Sutherland 1999; Berec et al. 2007; Courchamp et al. 2008; and references therein). Hence, a particular challenge to small founder populations is the reduction in intraspecific interactions based on changes in density following the introduction. This reduction produces a novel selection pressure that is endogenous and plays an important role in invader dynamics (Crooks 2005). Intraspecific interactions can mediate a positive relationship between measurable aspects of individual fitness, i.e., component Allee effects, and proxies of mean fitness, such as demographic Allee effects, i.e. per-capita population growth rate. This positive relationship can be manifested at the population level through the effects of per-capita growth rate on population size and persistence. Although component Allee effects influence individual fitness, whether or not demographic Allee effects are present and population dynamics are affected depends on the overall strength of the component effect, which can be mitigated by other, local

interactions and ecological processes (Gascoigne et al. 2009; Chapter 3). Further, since an Allee effect is a mechanism that affects individual fitness, it is subject to natural selection (Courchamp et al 2008; Gascoigne et al 2009). If there is some variability in the population with individuals better able to cope with the negative effects of low density, adaptation to low density across generations can effectively relieve the ecological constraints of density dependence – as long as the population is not too limited by demographic stochasticity in the short term.

Clearly, there is a close connection between what we often think of as ecological factors, such as Allee effects, and evolutionary ones, such as selection. In the context of Allee effects, both of these types of factors can influence invasion success and disentangling their relative contributions is complicated because single processes have both ecological and evolutionary implications. For example, time lags typically occur between the introduction of a species into a new area and a noticeable increase in population growth (Sakai et al. 2001) as observed in introductions of the house finch (Veit and Lewis 1996), zebra mussels (Johnson et al 2006), gypsy moths (Liebhold and Tobin 2006), and smooth cordgrass (Davis et al 2004). Such time lags have been explained through the ecological and evolutionary consequences of Allee effects in overcoming demographic constraints in order to establish and spread (Taylor and Hastings 2005; Courchamp et al 2008; Gascoigne et al 2009; Simberloff 2009). Various forms of rescue that can act during the time lag period are closely allied with the ecological and evolutionary effects that result in time lags (Crooks and Soule 1999; Simberloff 2009). Essentially, this interplay arises from the race between population

decline and the rate of adaptive evolution, as well as in the demographic and genetic contributions of immigrants on the size and fitness of the population.

In the context of evolutionary rescue, there is a growing body of work exploring the genetics and evolutionary potential of introduced species (Sakai et al 2001; Lee 2002; Cox 2004; Lambrinos 2004). Some of the clearest examples of rapid evolution come from introduced species (e.g., Quinn et al 2000) despite the notion that founder events can reduce genetic variation and thus hamper evolutionary change (Mayr 1954; Allendorf and Lundquist 2003). There is considerable evidence from microevolutionary studies that adaptive evolution occurs on contemporary timescales (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Ashely et al 2003; Rice and Emery 2003; Stockwell et al 2003) and it has been suggested that in altered environments, "rapid adaptation is the norm rather than the exception" (Stockwell and Ashely 2004). Evolutionary rescue is potentially important but the evidence is based on the few introductions that may have narrowly avoided extinction and obviously little is known about failed invasions. It is clear there are multifarious forces shaping the evolutionary dimensions of invasions, but again the relative role of these processes under the ecological constraints of introduction and Allee effects is poorly understood.

Despite the potential for rapid adaptation, the evolutionary trajectory of introduced populations is necessarily constrained by the ecological context of the endogenous selection pressure from Allee effects. Hence, ecological constraints and feedbacks on endogenous selection pressure may surprisingly limit and shape possible responses to selection. For example, in the context of component Allee effects, the local density of an individual impacts its fitness, so the spatial structure of populations

becomes very important. Ecological constraints arise because high dispersal decreases local density but also speeds the invasion process. Thus, there is a critical invasion area that must be occupied for establishment to be possible ecologically and this also places limits on the amount of dispersal of invaders (Skellam 1951; Kierstead and Slobodkin 1953; Okubo 1980; Lewis and Kareiva 1993; Kot 2001; Drury et al 2007; Verken et al 2011; Chapter 2).

Although evolutionary rescue alone has potential to explain invasion success, there is substantial evidence that additional introductions significantly increase the probability of establishment (Simberloff 2009). From the simplest ecological point of view, additional migrants can bolster the population size and help buffer against Allee effects, over-dispersal and demographic and environmental stochasticity through demographic rescue (Brown and Kodric-Brown 1977). However, even if an immigration event pushes the population above the demographic Allee threshold, this may not be sufficient for a demographic rescue effect due to the implications of the critical invasion area criteria (Drury et al 2007). Even when increased propagule pressure is insufficient for demographic rescue to occur, the addition of conspecifics can introduce beneficial alleles resulting in genetic rescue and/or increased genetic variation that facilitates adaptive evolution and evolutionary rescue (Thrall et al 1998). This effect is certainly dependent on the degree of genetic divergence between the founder and immigrant populations, but additional migrants may nonetheless extend the time lag allowing for the demographic and genetic effects to work in concert and promote adaptive evolution (Tallmon et al 2004).

To better illustrate the interplay between ecological and evolutionary processes that influence persistence of a founder population subject to Allee effects, we present a conceptual framework that demonstrates the relative effects and consequences of evolutionary, demographic, and genetic rescue (Figure 1). Since the intensity of the selection pressure and individual fitness is governed by intraspecific interactions and population density, we consider the evolution of an ecologically important quantitative trait that governs the influence of population size on fitness. Therefore, the trait value is a phenotypic measure of the strength of component Allee effects, where maladapted individuals with low fitness are in a population that is smaller than their trait value. Variation around the mean phenotype (demonstrated by arrow a, measuring the width of the distribution) is important in maintaining reproductively active individuals and preventing immediate extinction. Individuals that are better adapted to the small population size (in region b) reproduce, which may not have any net effect on population size due to die off of maladapted individuals. However, the trait distribution can subsequently shift in the direction of evolution (indicated by arrow d). This process would lead to evolutionary rescue without additional immigrants. With additional immigrants, rescue may be hastened. If there is a significant increase in population size (in the direction of arrow c) beyond the mean phenotype, demographic rescue occurs. However, if the population size does not increase dramatically, the addition of new individuals can widen the trait distribution with new variation (arrow a) or actually shift the mean phenotype with the introduction of beneficial alleles (arrow d), resulting in genetic rescue. Hence, we consider the relative importance of these effects in contributing to rescue from extinction in the face of ecological constraints on population

growth, and furthermore incorporate the effects of mutation and recombination on the trait variation (arrow a).

We developed a spatially explicit individual-based model that incorporates both demographic and genetic stochastic processes in order to determine the relative importance of the different forms of rescue in mitigating Allee effects in a small founder population. We track multi-locus genotypes of individuals to investigate how initial genetic variation coupled with the effects of mutation and recombination affect the rate of adaptive evolution when the selection pressure varies with population size. Additionally, we assess the influence of immigration events on demographic and genetic processes and determine the relative contribution of these factors to the overall likelihood of rescue and subsequent invasion. Finally, we address the contribution of different sources of genetic variation to evolutionary rescue and determine how much evolutionary rescue depends on initial genetic variance versus mutation and recombination.

Model Description

Our model operates from a bottom-up perspective and focuses on how intraspecific interactions and density mediated fitness drive population dynamics. We took a novel approach in considering the factors influencing persistence by concentrating on the endogenous environment as opposed to the exogenous habitat where selection is based on trait matching with a fixed optimum (e.g., Gomulkeiwicz and Holt 1995). We expanded on the demographic framework previously used to examine the effect of endogenous spatial heterogeneity on intraspecifc interactions (Chapter 3) to explicitly incorporate quantitative genetic structure (Burger and Lynch 1995; Holt et al 2003). Comprehensive computer simulations were performed in order to deal with multiple

stochastic effects (e.g., mutation, recombination, genetic variation, dispersal, and the demographic birth-death process).

Ecological assumptions

A small population of diploid, sexually reproducing, hermaphroditic individuals was introduced into a continuous space environment within a specified area and spatial distribution. We use Gillespie's Direct algorithm to simulate a continuous time birth-death process (Gillespie 1977; Renshaw 1991; Birch and Young 2006; Erban et al. 2007; Chapter 3). For each individual, i, their current birth (b_i) and death (d_i) rates were determined by taking into account the number of conspecifics in their local neighborhood, N_i, (with a specified local interaction kernel, e.g., top-hat with radius 1 for these simulations) along with their phenotypic value for strength of Allee effects, a_i, and local carrying capacity, K (Chapter 3).

$$b_i = \frac{N_i}{a_i} + \frac{N_i}{K} = \frac{N_i(a_i+K)}{a_iK}, \quad d_i = 1 + \frac{N_i^2}{a_iK} = \frac{a_iK+N_i^2}{a_iK} \tag{1}$$

These relations used for birth and death rates were derived (similar to those in Ackleh et al. 2007; Chapter 3) from a well-studied, reaction-diffusion model (Lewis and Kareiva 1993; Murray 1993; Keitt et al 2001; Kot 2001; Drake et al 2005; Drury et al 2007; Chapter 2) that represents the standard dynamics of strong Allee effects. Since births and deaths are assumed to be independent Poisson processes, the sum of the birth and death rates can be summed over all individuals to give an overall event rate E for the entire population. The time until the next event (birth or death) is exponentially distributed with a mean of $1/E$. The event is chosen to be a birth or death based on the probability of a birth or death occurring in the population, and an individual is then chosen to reproduce or die based on the magnitude of that individual's respective probability. Upon

reproduction, an individual, i, randomly chooses a mate, j, within their local neighborhood. Each parent produces a gamete according to particular genetic assumptions (below) and one offspring is produced at the location of parent i. All individuals in the population then move in a random direction with normally distributed distance with mean 0 and variance $2D\Delta t$ (where Δt is the inter-event time and is sufficiently small approximating continuous movement, and D is the diffusion coefficient given in Table 1; Birch and Young 2006; Twomey 2007; Chapter 3). This process continues until the population goes extinct or grows sufficiently large that persistence is reasonably certain. From preliminary results, persistence was reasonably certain when the population size was greater than 100 individuals, and we used this as our cutoff.

Immigrants are introduced in the same way and reproduce and move according to the algorithm above. Other work has investigated invasion risk with multiple introductions of varying spatial proximity to the original release point (Drury et al 2007). In light of these results, we took a straightforward approach and fixed the introduction site and focus on the number of immigrants and arrival time. We simulated an immigration event by introducing a fixed number of individuals after a particular amount of time has elapsed (see initial conditions and parameters). Immigrants immediately contribute to the birth-death process of the existing population.

Genetic assumptions

Selection acts implicitly in our model on the strength of an individual's component Allee effects, determined by the difference between their local population size, N_i, and their phenotypic value, a_i. This difference influences the chances of reproduction and survival (Chapter 2). We model the fitness governing quantitative trait,

a_i, with a multi-locus approach because many traits of ecological importance in natural populations are polygenic (Falconer and MacKay 1996). The polygenic character a_i is determined by n diploid loci, with additive allelic effects within and among loci (i.e., with no dominance or epistasis). We found little quantitative difference among simulation results with the number of loci $n \geq 5$ similar to Holt et al. (2003). Therefore, we set n equal to 5 loci, and each individual has $2n$ alleles. We allow the number of possible segregating alleles per locus to be limited only by population size (Kimura and Crow 1964; Burger 1999). The initial founder population is initialized with allelic values chosen at random from a normal distribution with mean, $\bar{a}/2n$, and variance, σ^2_g. We use phenotype and genotype interchangeably, because the phenotypic value for each individual is based on the sum of the genetic allelic values. Also note that genetic variance is per haplotype locus, thus the total additive genetic variance is $2n\ \sigma^2_g$.

We examined the impact of recombination by allowing loci to freely recombine. In simulations that include the effects of recombination, each parent randomly contributes one allelic value for each locus from their diploid genome to their gamete. Without recombination, one haplotype is randomly chosen. We do not constrain the set of alleles that may be present in the population, and allow new alleles to appear through mutation. The mutation rate per haplotype is $n\mu$ where μ is the mutation rate per locus (Burger and Lynch 1995; Holt et al 2003). Following segregation and assortment, up to one mutation may occur (per haplotype) at a randomly chosen locus. Under mutation, the mutation size is normally distributed with mean zero, variance α^2 and is added to the previous allelic value.

Parameters and initial conditions

We initialize 25 individuals at the start of each simulation with an expected phenotypic mean ($\bar{a}$) of 25 (unless otherwise noted) such that each introduced population is at the demographic Allee threshold (the unstable equilibrium for critical size; Chapter 2; Chapter 3). We kept the mutation rate and variance constant (and used values based on Holt et al 2003; where $n\mu = 0.01$ and $\alpha^2 = 0.05$) in order to standardize the initial genetic variance across simulations (where $\sigma^2_g = 0.05$; but see Appendix A and B for the effect of varying these parameters). The basis for this standardization is the approximation for the expected stochastic 'house-of-cards' for genetic variance at equilibrium (Burger et al 1989; Burger and Lynch 1995).

The size of the immigrant population was fixed at 15 and introduced when the sum of inter-event times was approximately one to make broad comparisons with immigration (see Appendix C for the effect of varying these parameters). Genetic variance, mutation and recombination parameters for immigrants were the same as the founder population; however we did vary the expected mean phenotype of the immigrant population from well adapted (i.e., $\bar{a}_{imm} = 20$) to the same as the founder population (i.e., $\bar{a}_{imm} = 25$) to maladapted (i.e., $\bar{a}_{imm} = 30$).

Finally, we found in Chapter 3 that the interaction between dispersal distance and spatial structure can qualitatively influence population dynamics during introduction in this type of scenario. Hence, we preliminarily explored multiple combinations of these characteristics based on our previous work, but used fixed values for the presentation here. Thus, the diffusion coefficient, D, was set at 0.01 and initial spatial structure measured by Ripley's K, a clustering statistic (Ripley 1976), was similar for each run (with moderate heterogeneity where $\widehat{K}_0 \approx 2.0$; Chapter 3). These values produce an

ecological context where individuals do not disperse too quickly giving sufficient time to extinction for the opportunity for rescue to exist (see the results of the 'null' model).

The entire model comprising ecological and evolutionary consequences of Allee effects in small founder populations (with and without additional immigration) has multiple sources of stochasticity. Therefore, 1000 replicates were performed across a range of parameter values to tease apart the relative contribution of various components of the model and better understand the sensitivity of the dynamics to different assumptions (see Appendix). We then fixed particular parameters to draw comparisons and elucidate the primary drivers of population success. In the following results, we compared three main model types for populations with and without initial genetic variance: (1) without mutation or recombination (the 'null' model), (2) with mutation only, and (3) both mutation and recombination (hereon referred to by recombination). We used this same comparison structure to assess the impact of immigration. We quantified the proportion of successes (i.e., establishment and persistence through positive population growth) and looked at average time to extinction (i.e., as a proxy for the time lag which is difficult to objectively quantify). We also tracked the initial phenotypic trait distribution as well as the change in the population size, mean phenotype and variance over time.

Results & Discussion

We diagram the individual fitness surface, relating the phenotype for component Allee effects, a_i, to local population size, N_i, to gain a better sense of the ecological and evolutionary forces influencing model results. Based on eqn. 1, we use the difference between the probability of birth ($\frac{b_i}{b_i+d_i}$) and the probability of death ($\frac{d_i}{b_i+d_i}$) as a measure

for individual fitness (r_i). In Figure 2, the dot represents an individual with the default initial conditions in the model, $a_i = 25$, $N_i = 25$. Hence the initial probability that the individual reproduces is equal to the probability that it dies. The fate of the individual is highly sensitive to its local, neighborhood population size due to the density dependent fitness function. Thus, because of constant fluctuations in the individual's local population (as birth, immigration, death, and movement occur), an individual's fitness is always changing along the short dashed line (where a_i remains constant). This fast-paced ecological process caused by demographic feedbacks is by definition how Allee effects are expressed (i.e., as an increase in fitness with population size, Courchamp et al 2008). If the individual's local population size exceeds its phenotypic value for the strength of component Allee effects (i.e., threshold where birth probability exceeds death probability), the individual has a better chance of reproducing and surviving. The demographic processes that impact the individual described in Figure 2, scale up to impact the probability of demographic rescue at the population level. To better understand how individual fitness impacts evolutionary and genetic rescue, we must consider multiple individuals on this fitness surface. Given the default values for expected genetic variance (Table 1), at the start of a simulation with variation, individual phenotypic values can fall in the range of the error bar shown on the point in Figure 2 along the a_i axis. Because the surface is flatter along the a_i axis, phenotypic variation in a_i confers a smaller fitness advantage than fluctuations in local population size caused by ecological processes. The relative steepness of the individual fitness surface with respect to phenotypic factors (a_i) versus ecological factors (N_i) foreshadows the importance of demographic rescue versus other types of rescue at the population level. Overall, an

individual has a greater expected fitness when $a_i < N_i$ (where $b_i > d_i$ in the upper half of the surface that is darkly shaded). Scaling up from individual-level fitness to population dynamics, we first highlight the relative effect of each type of rescue given various sources of genetic variation by presenting comparisons of mean behavior. We then illustrate major trends with representative model runs.

We used the baseline 'null' model to understand the impact of the stochastic birth-death process on persistence and extinction. Figure 3a demonstrates that 10% of the introduced populations can succeed as a result of the stochastic birth-death process alone (Chapter 3).

Comparison of the dark bars in Figure 3a shows that neither mutation nor recombination contribute strongly to evolutionary rescue as the proportion of successes does not increase meaningfully under these models. Mean phenotype follows a similar pattern (Figure 3b). Interestingly, Figure 3c reveals that the small decrease in mean phenotype under recombination is enough to increase the mean time to extinction, although not the ultimate outcome of extinction.

Founder populations with genetic variation do generate a higher proportion of successes suggesting evolutionary rescue does occur (i.e., null model with variation compared to without, Figure 3a). In this case, the mean phenotype for the successful populations decreased (Figure 3b) but the mean time to extinction was unaffected (Figure 3c). Mutation added to initial variation (Figure 3b) resulted in a greater number of successes (Figure 3a) and a slightly increased mean time to extinction (Figure 3c). Not surprisingly, the effect of recombination lead to a greater likelihood of success because it generates the most genetic variation of the processes considered (Figure 3a), although the

mean phenotype and variance are not markedly different with the addition of recombination (Figure 3b). It is obvious that phenotypic values less than 25 are advantageous, but once rescue occurs, the strength of selection diminishes drastically and the phenotype stops changing. Interestingly, we also observed that the mean time to extinction increases from the null model to the model with recombination. This extended time to extinction suggests that although the rate of evolution may not significantly increase, additional time can provide the opportunity for beneficial alleles and allelic combinations to emerge resulting in a greater proportion of successful populations where recombination and mutation occur.

In assessing the added impact of immigration, we first note that approximately 40% of the model replicates succeed for populations without variation and with the addition of identical immigrants (Figure 4a). Compared with the 'null' model (without variation) in Figure 3a, this means that demographic rescue accounted for a 30% increase in likelihood of persistence beyond the baseline effect of demographic stochasticity. In a similar way, we use the results from Figure 3 to interpret the additional genetic impact of immigrants and assess the occurrence of genetic rescue. Overall, similar general trends appear in the mutation and recombination models with and without initial variation and with and without immigration (first two bars for each model type, Figure 3 and Figure 4). The immigrant population had allelic values drawn from the same distribution as the resident population in these cases. Thus, it is not surprising that immigration had little impact. We observed approximately the same 30% increases in the proportion of successes (Figure 3a compared with Figure 4a), and we consider this a combination of demographic rescue with adaptive evolution rather than genetic rescue.

The potential effect of the genetic contribution from the immigrant population is primarily demonstrated when the mean trait values differed from the original founders. In Figure 4, the latter two bars for each model type show the results for better-adapted immigrants and maladapted immigrants with the same initial variance. In the case of better-adapted immigrants, the increases in the proportion of success represent genetic rescue (Figure 4a). The additional introduction of maladapted individuals is detrimental and constrains adaptive evolution. We further evaluate the impacts of phenotypic divergence in the immigrants and the effect of timing of immigration in Appendix C.

We specifically illustrate some of the dynamics giving rise to the results for evolutionary, demographic and genetic rescue in order to better understand these broad comparisons. Figure 5 shows characteristic examples of evolutionary rescue. In each scenario, there was no initial genetic variation in order to represent how variation emerges through mutation and recombination. The null model population is driven by demographic stochasticity. The mutation and recombination models show extended time lags related to the amount of genetic variation generated by each process.

Figure 6 illustrates that demographic rescue is not just based on the number of immigrants and time of introduction, but also hinges on the trajectory of population size and how the invasion develops (e.g., spatial distribution). The impact of the ecological conditions is illustrated by the very different trajectories under demographic rescue of two populations that have the same simulation parameters. Figure 7 shows examples of genetic rescue. In this example, we manipulated which individuals were chosen for the immigrant populations in order to clearly illustrate the consequences of the level of adaptation in the immigrants. In one model run we chose immigrants with maladapted

phenotypes ($a_i > 25$), and chose well-adapted immigrants ($a_i < 25$) for the other. Both founder populations perform with similar behavior until the immigration event (Figure 7a). At that time, the trait means diverge significantly with roughly the same variance (Figure 7b), and either swamp the population with reduced survival and reproduction due to elevated necessity for intraspecific interactions and stronger component Allee effects resulting in extinction or genetically rescue the population by introducing beneficial alleles facilitating evolution.

Conclusions

A small, introduced population with Allee effects can only succeed if faced with favorable ecological conditions, the ability to undergo rapid adaptive evolution, or luck. Our stochastic simulations produced all three possibilities and allowed us to quantify their relative importance for invasion success. Beyond the 10% of successes not attributable to any rescue effect, additional immigration had a stronger impact on overcoming density dependence than evolution alone due to the shape of the individual fitness surface. For example, the addition of 15 immigrants early on had the same effect on establishment success as a founder population with five times more additive genetic variance than the default value used (Figure A1). The impact of immigration was largely through demographic rescue, as opposed to genetic rescue. Once demographic rescue occurred, we did not find that additional immigration enhanced local adaptation, which is in contrast to other studies of evolution in source/sink environments (e.g., Holt et al. 2004). Local adaptation ceases following demographic rescue in our model because intraspecific interactions are the source of endogenous selection pressure. Once populations are above the Allee threshold by any means, the selection pressure ceases.

Thus, there was little difference between evolutionary change with or without additional immigration, except when the immigrants were divergent enough to shift the mean phenotype and generate a genetic rescue effect. Overall, the increased effect of demographic rescue over evolutionary and genetic rescue is a general consequence of strong Allee effects as illustrated conceptually in Figure 2 and is broadly applicable beyond the scope of this investigation.

In the context of our model, not only is there an abbreviated time scale during which evolution can occur, there are other implicit genetic consequences of small populations and Allee effects. The most obvious is the potential reduction of diversity due to genetic drift and founder effects; however there is much recent evidence that indicates that the typical loss of additive genetic variance is minimal (Lee 2002; Wares et al. 2004; Shi et al 2010). Kramer and Sarnelle (2008) even suggest that Allee effects may lead to resistance to significant changes in heterozygosity and genetic distance by imposing limits on minimum population size. Specifically, they found that 70-75% of populations of an alpine copepod that maintain the minimal population size lost <10% of allelic richness. Although it seems that the ecological limitations that Allee effects have for critical density can actually maintain genetic variation, we suspect that the spatial constraints influencing population growth can actually limit genetic variation through limited mating options. This is also consistent with Kramer and Sarnelle's (2008) analysis that increased habitat size of a founder population at critical density also increased the proportion of original allelic richness. Thus, in the race against time for evolution to reduce component Allee effects through heritable fitness related traits, endogenous spatial heterogeneity that emerges ecologically to mitigate component Allee

effects (Chapter 3) may limit the amount of genetic variation and further slow the process of evolutionary rescue. Even though there may be sufficient genetic variance in the founder population, spatial structure may render it inaccessible and lead to a tug-of-war between ecological and evolutionary survival mechanisms.

The mounting empirical evidence of adaptive evolution following invasions (Huey et al 2000; Thomas et al 2001; Sexton et al 2002; Lee et al 2003, 2007; Blair and Wolfe 2004; Cox 2004; Maron et al 2004; Muller-Scharer et al 2004; Bossdorf et al 2005; Gilchrist and Lee 2007) must be reconciled with these results. One reasonable reconciliation is that establishment and persistence are relatively rare compared to the number of introductions that fail (Williamson and Fitter 1996). Our results then suggest that because of demographic constraints on the evolutionary dynamics, the probability of evolutionary rescue is low and the observed examples are rare events. This explanation is consistent with the paradox of evolutionary rescue, where stronger selection gives rise to faster evolution while imposing a greater demographic cost and risk of extinction (Kinnison and Hairston 2007). We chose to exemplify this scenario by incorporating strong (as opposed to weak) Allee effects that produce an extinction threshold with negative growth (Berec et al 2007). Thus, the time to extinction is drastically hastened as soon as the population falls below the mean phenotype (i.e., Allee threshold). Evolutionary processes would play a more dramatic role in this simulation framework if a weak Allee effect or a more substantial fitness advantage from a small phenotypic change were incorporated. Hence, an alternative reconciliation of our results with empirical evidence is that strong Allee effects are necessarily rare in successful introductions.

To further assess the relevance of evolutionary processes, it might be helpful to take a more empirical approach in characterizing how density dependence operates at low densities and determining which mechanisms generating Allee effects are under selection, the probability of adaptation given the mating system, and whether the adaptations allow persistence at low density or serve to increase density (Holt et al 2004; Gascoigne et al 2009). There are a number of examples of the selective pressures that Allee effects exert on invasive species. The evolutionary response is primarily adaptations facilitating reproduction by altering mating systems (e.g., self-fertilization, Taylor and Hastings 2005; reproductive timing, Barrett et al 2008; induced ovulation, Jabbour et al 1994; parthenogenesis, Hopper and Roush 1993; masting, Koenig and Ashley 2003; gamete morphology and performance, Levitan 2002; and other life history traits, Gascoigne et al 2009) and those that additionally affect survival, including detection of conspecifics as well as dispersal characteristics (Wells et al 1998; Travis et al 2005). In one of the most direct studies, Elam et al (2007) found that in self-incompatible invasive wild radishes that population size and genetic relatedness influence maternal reproductive success, and suggest that multi-seeded fruits are an apparent adaptation to overcome the challenge of an Allee effect. Overall, understanding the ecological attributes of the mating system and dispersal mode can offer powerful insight into evolution, invasiveness and establishment likelihood of small populations.

Our results are broadly applicable to a wide variety of taxa and emphasize the complex reality facing a small founder population. Our model captures the evolutionary phenomenon of adaptations influencing intraspecific interactions as opposed to acclimating to the exogenous environment in order to demonstrate the demographic

challenge posed by Allee effects. When fitness is depressed at small population sizes, the ecological, evolutionary, and genetic obstacles that successful invaders need to overcome are exacerbated. Our results not only highlight potential mechanisms and conditions facilitating or hampering rapid adaptive evolution and establishment success of small founder populations, but also provide phenomenological insight on how Allee effects contribute to the paradox of invasion.

Table 1

Parameters , definitions and values used			
Parameter	Definition	Range	Default
n	Number of loci	1 - 10	5
$n\mu$	Mutation rate per haplotype	10^{-6} - 0.1	0.01
α^2	Mutational variance	0.01 - 0.1	0.05
σ^2_g	Genetic variance per haplotype locus	0.01 - 0.25	0.05
$\bar{a}$	Initial mean phenotype, Allee threshold	25	25
$\bar{a}_{imm}$	Mean phenotype Allee threshold of immigrants	20-30	20,25,30
I_t	Time of immigration event	1-10	1
I_n	Number of immigrants per event	1-25	15
K	Carrying capacity	100	100
D	Dispersal distance	0.001 - 0.1	0.01
$\widehat{K}_0$	Ripley's K for initial spatial distribution	1.4 - 2.4	2.0

Figure 1: Conceptual representation of the basic elements driving evolutionary, genetic, and demographic rescue. The population's trait values are normally distributed centered around the mean phenotype (i.e., average Allee threshold) with variance impacting the width of the distribution (arrow a). The distance between the population size and the mean phenotype is the degree of maladaptation. The individuals in shaded region b, have better-adapted phenotypes with trait values that fall below the population size. If those individuals successfully reproduce enough prior to population extinction, the population size can shift right (arrow c) and the mean phenotype will shift left (arrow d) beginning the trend toward evolutionary rescue. Demographic rescue is caused by the addition of new immigrants that push the population size (arrow c) beyond the mean phenotype. Genetic rescue occurs when the contribution of immigration enhances the variance (arrow a) and primarily shifts the mean phenotype to the left (arrow d). All of these forces can operate simultaneously.

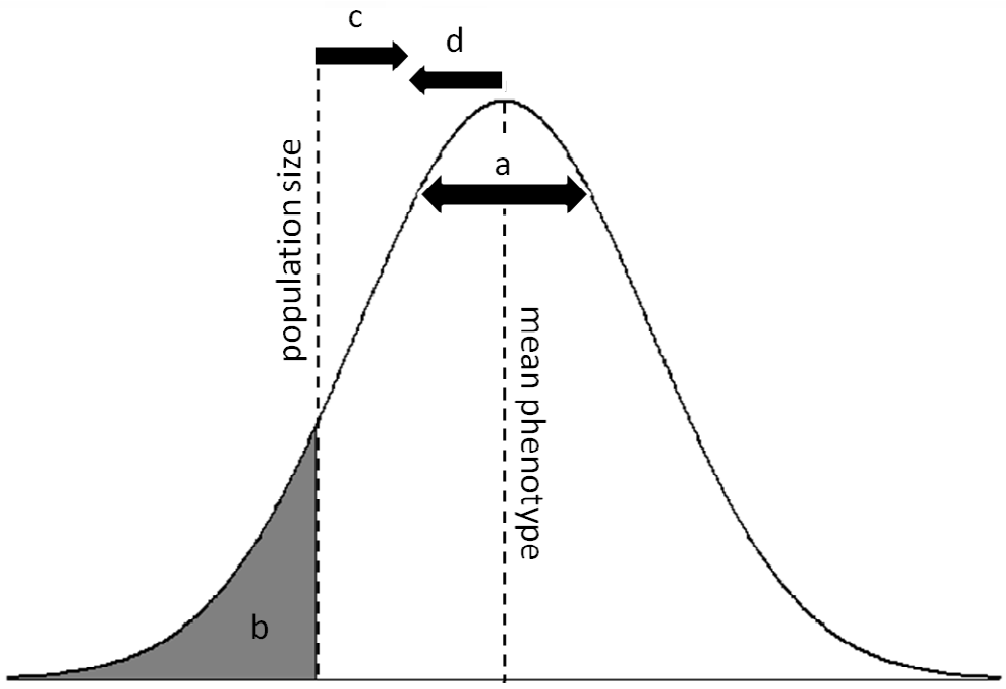


Figure 2: Individual fitness surface where fitness is the difference between birth and death probabilities and is a function of the individual phenotype (a_i) and local population size (N_i). An individual, represented by the dot, has an equal probability of birth or death when the trait value equals the population size (along the long dashed line). The error bar represents the range of phenotypic values an individual could be initialized with. Fluctuations in local population size will move the individual along the short dashed line, indicated by the arrows. Individuals in the darker region are well-adapted, while those in the lighter region are maladapted.

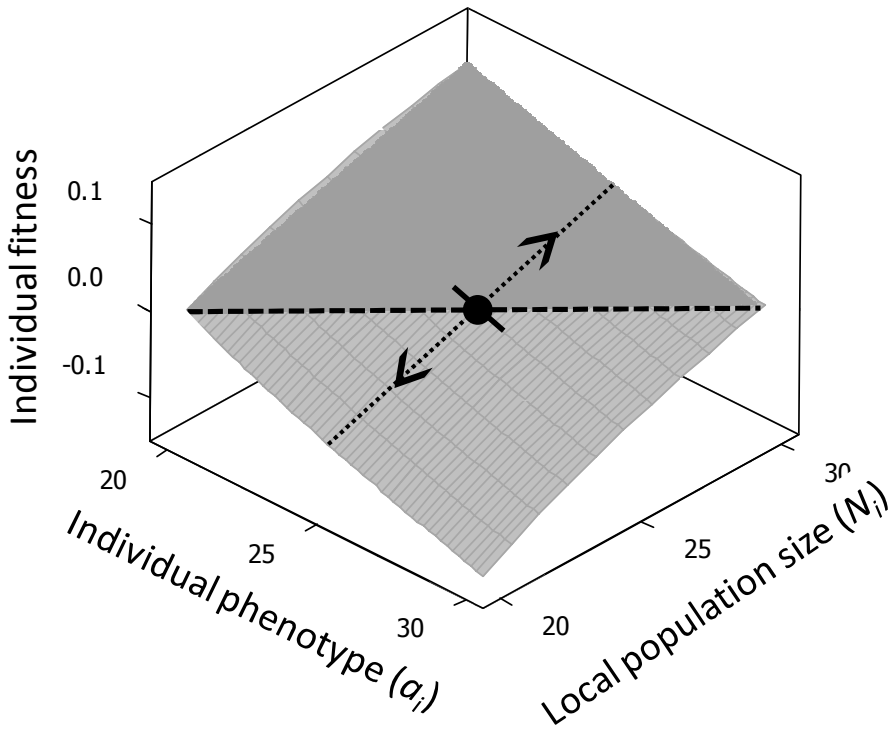
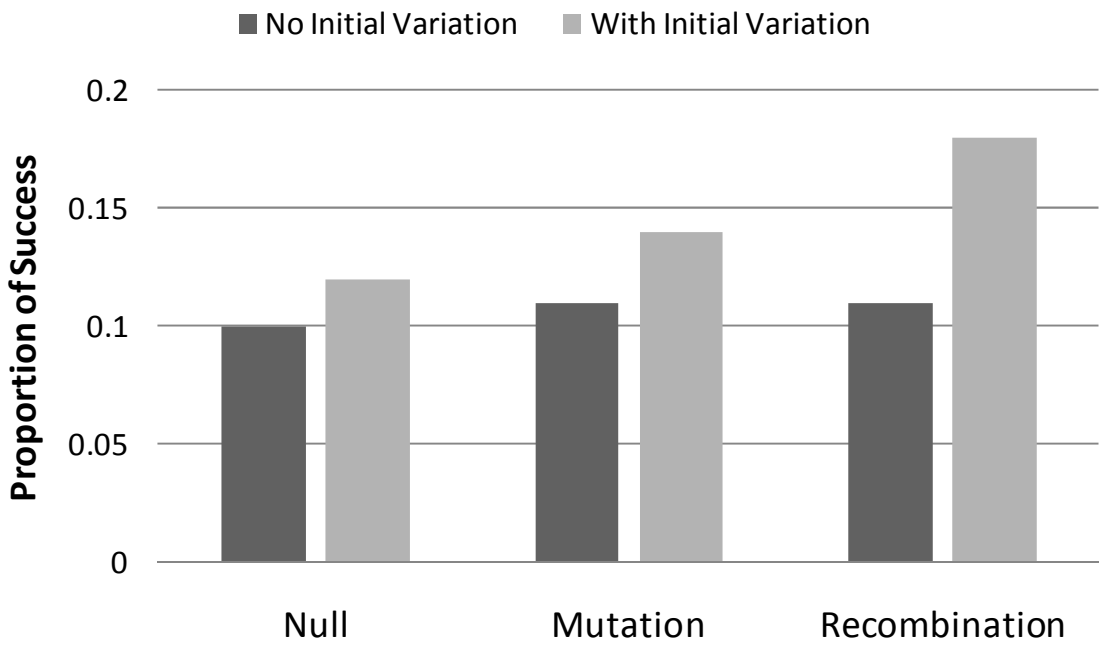
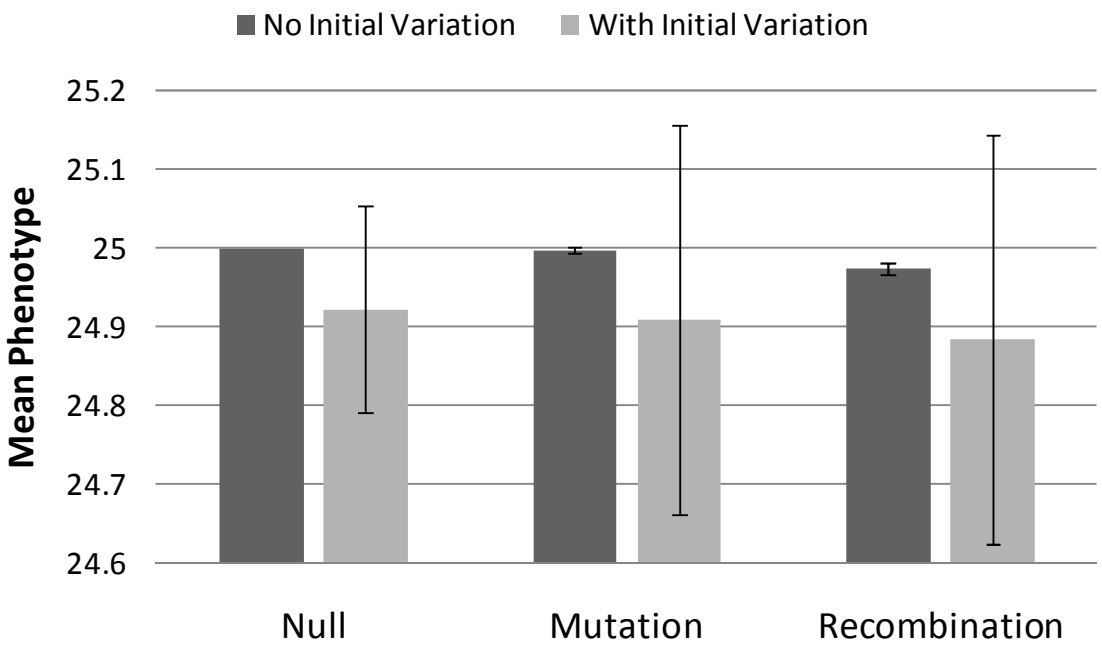


Figure 3: Comparisons between different sources of genetic variation with (dark grey bars) or without (light grey bars) initial variance. The null model has no variance generating processes. (a) The proportion of populations that have succeeded of 1000 replicates. (b) The average phenotype of successful populations (error bars are total additive variance). (c) The average time to extinction (error bars are one standard deviation).

(a)



(b)


No Initial Variation
With Initial Variation
Mean Phenotype
25.2
25.1
25
24.9
24.8
24.7
24.6
Null
Mutation
Recombination

(c)

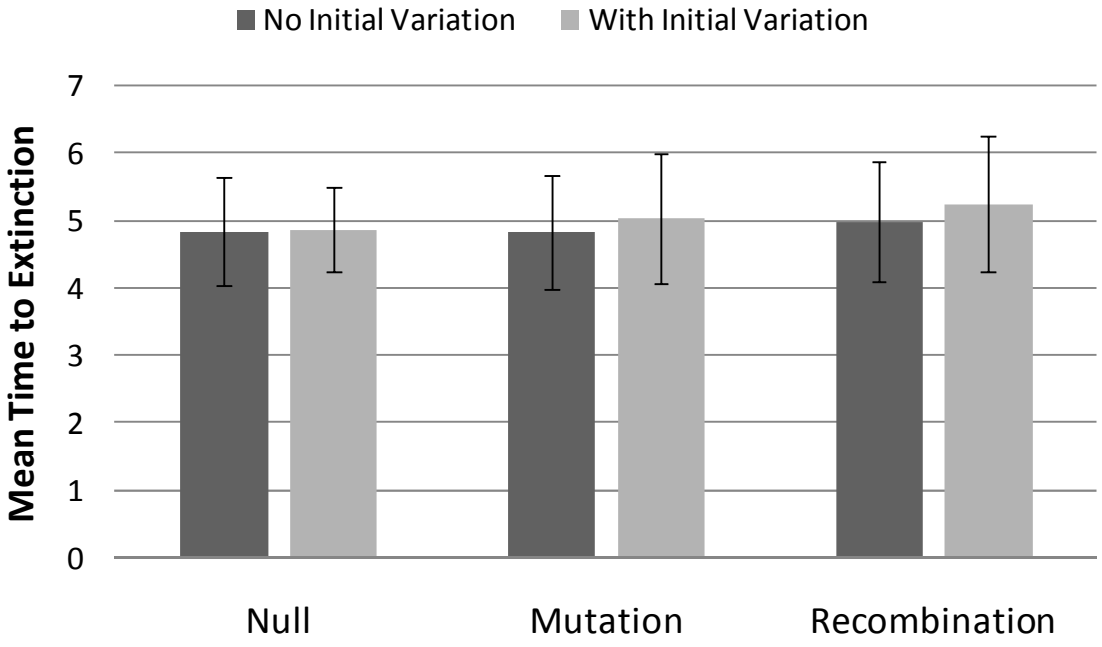
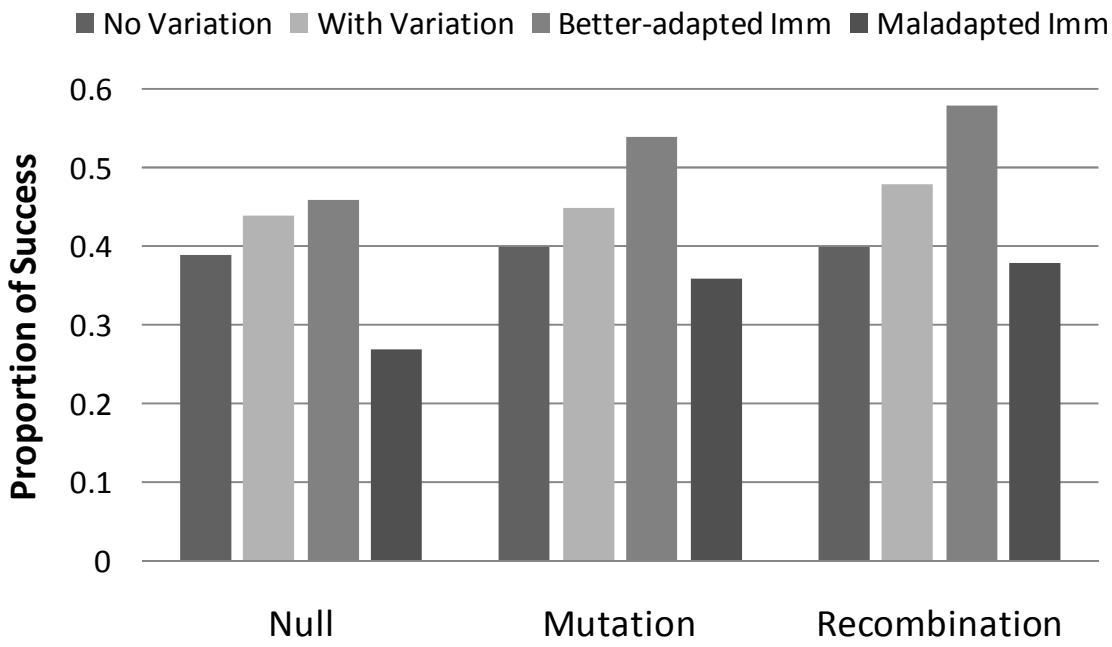
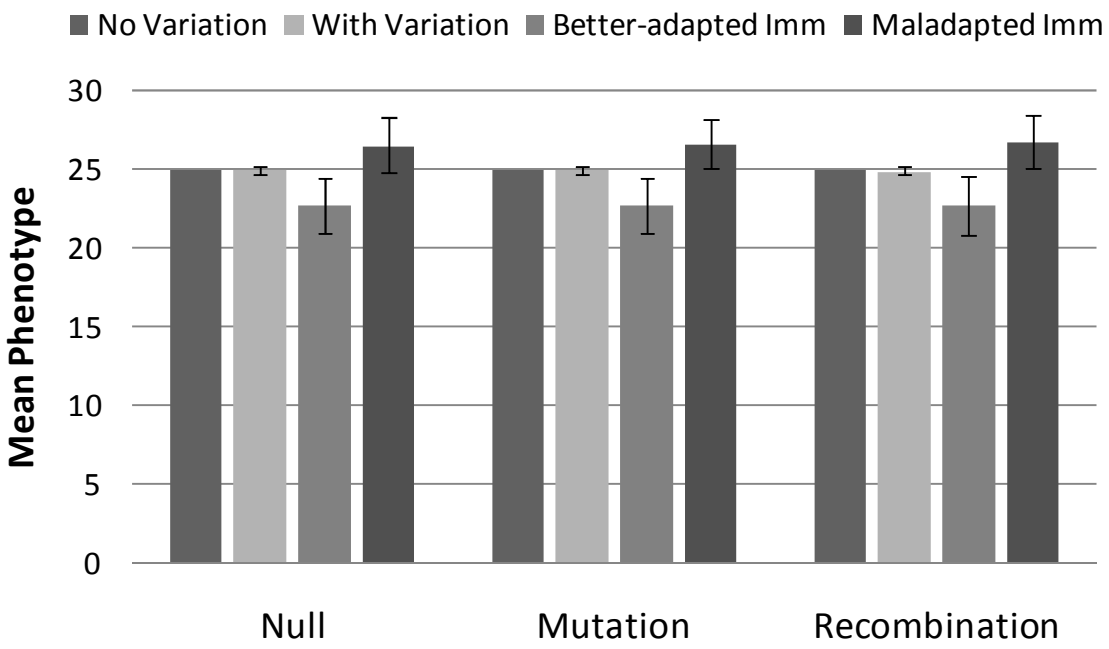

No Initial Variation
With Initial Variation
Mean Time to Extinction
7
6
5
4
3
2
1
0
Null
Mutation
Recombination

Figure 4: Comparisons between different sources of genetic variation with or without initial variance and immigration ($\bar{a}$ = 25 and $\bar{a}_{imm}$ = 20 for better-adaptive immigrants and $\bar{a}_{imm}$ = 30 for maladaptive immigrants). Selection acts on the variants within the three models: (1) the null model has only standing variation, (2) mutation only, or (3) mutation and recombination contribute to variation. (a) shows the proportion of populations that have succeeded of 1000 replicates, (b) gives the average phenotype of successful populations (error bars are one standard deviation), and (c) gives the average time to extinction (error bars are one standard deviation).

(a)



(b)


No Variation
With Variation
Better-adapted Imm
Maladapted Imm
Mean Phenotype
30
25
20
15
10
5
0
Null
Mutation
Recombination

(c)

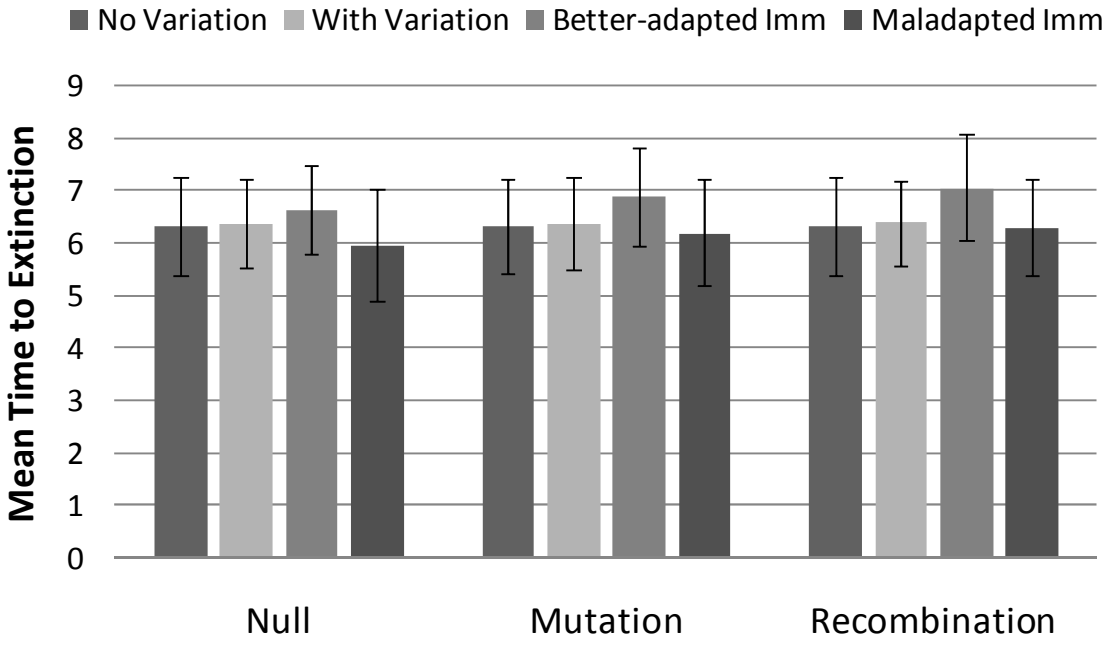
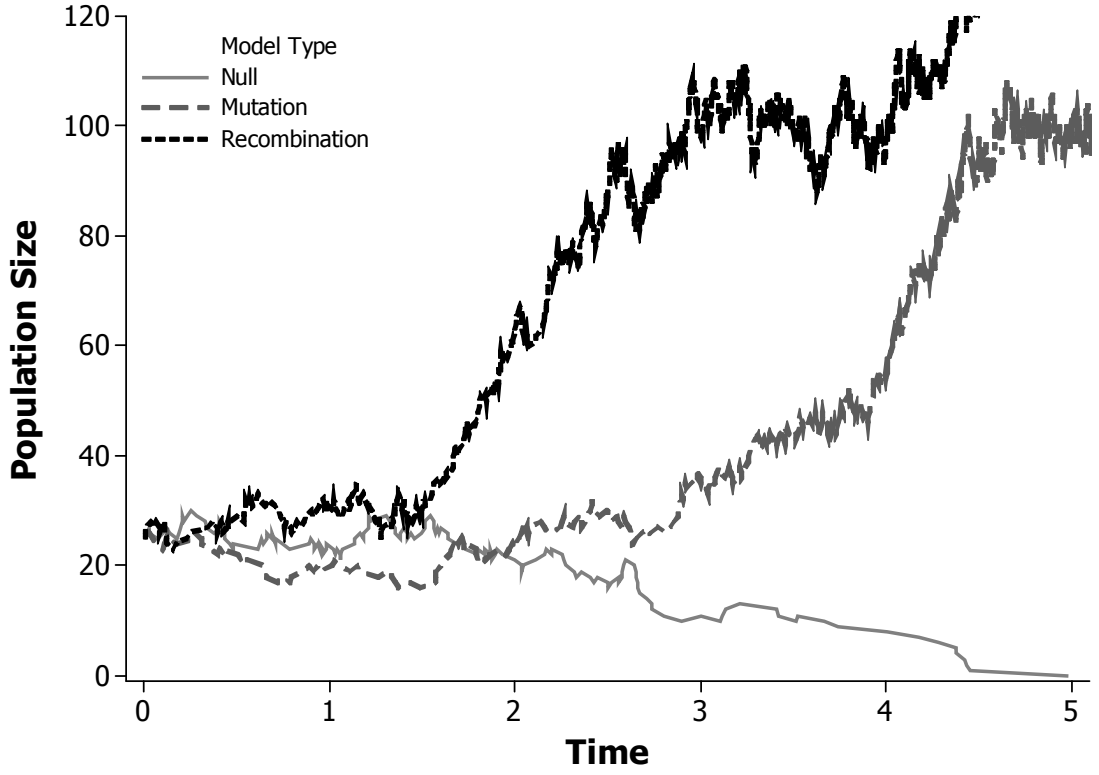

No Variation
With Variation
Better-adapted Imm
Maladapted Imm
Mean Time to Extinction
9
8
7
6
5
4
3
2
1
0
Null
Mutation
Recombination

Figure 5: Representative trajectories for (a) population size and (b) mean phenotype (Allee threshold). In (b), dark lines show dynamics of the mean and light lines indicate the associated range of genetic variance.

(a)



(b)

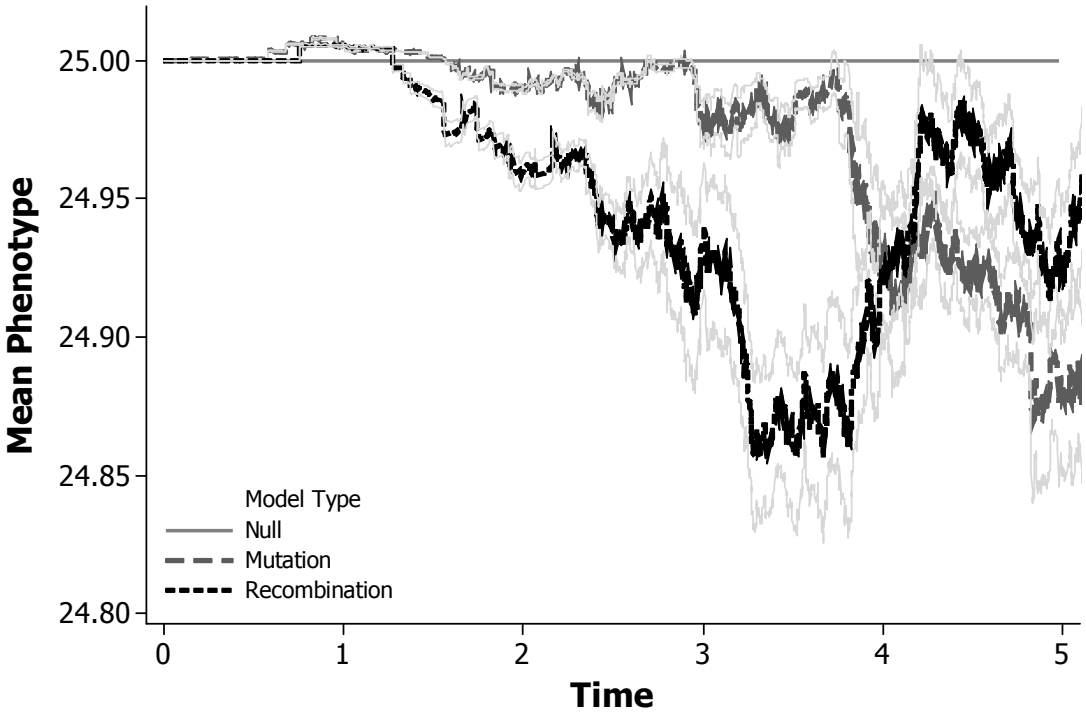

Mean Phenotype
25.00
24.95
24.90
24.85
24.80
0
1
2
3
4
5
Time
Model Type
Null
Mutation
Recombination

Figure 6: Representative trajectories of population size over time with an immigration event of 15 individuals occurring at approximately Time 1 as indicated by the arrow. The dashed line illustrates demographic rescue. There was no genetic variation and hence, no evolution.

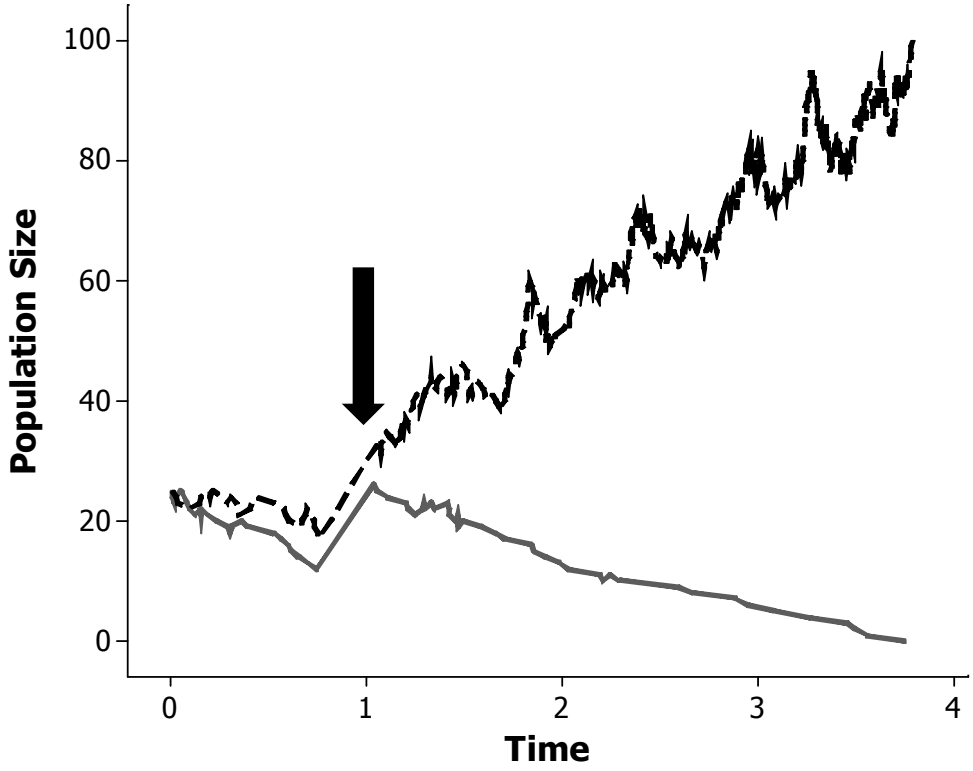
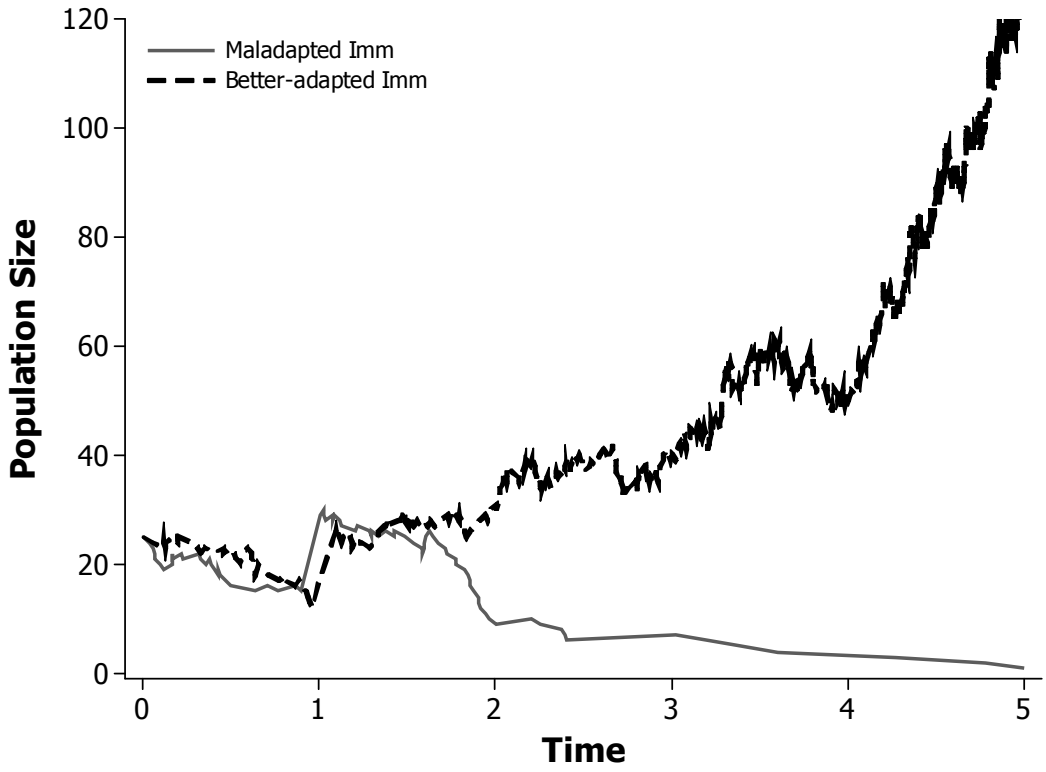
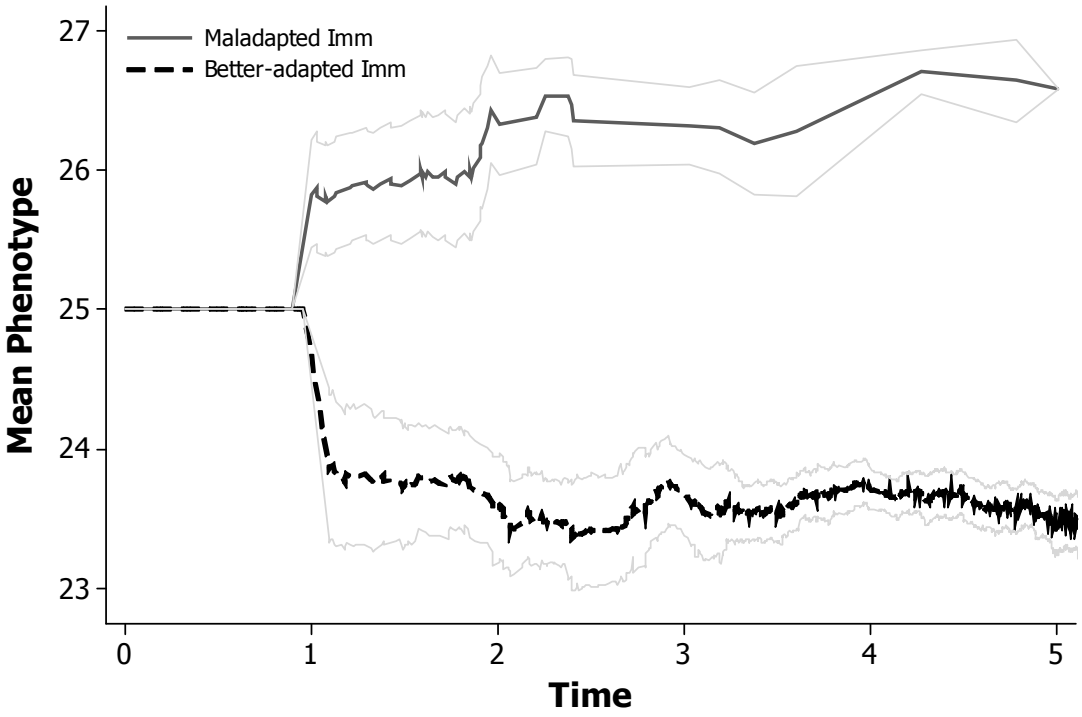


Figure 7: Representative trajectories of (a) population size and (b) mean phenotype and genetic variance (light grey lines following means) over time with immigration. These simulations included mutation and recombination and further variation was introduced by immigration. The dashed trajectories illustrate genetic rescue.

(a)



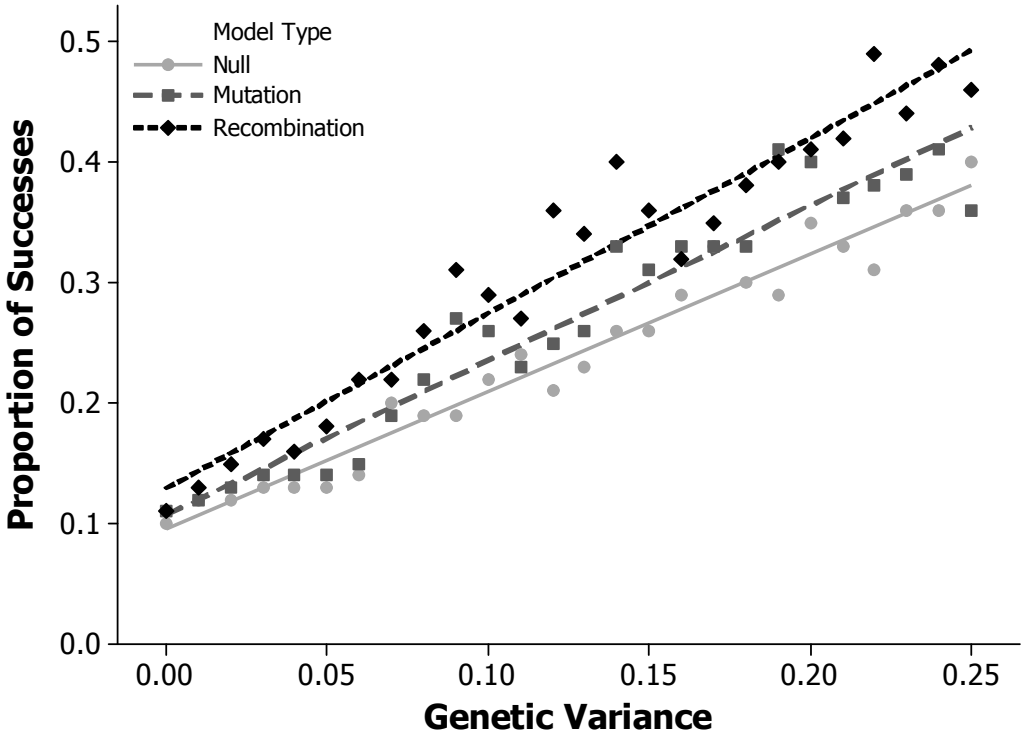
(b)


Maladapted Imm
Better-adapted Imm
Mean Phenotype
27
26
25
24
23
0
1
2
3
4
5
Time

Appendix A: Impact of initial genetic variance

In general, an increase in mean fitness is proportional to the additive genetic variance in a population (Fisher 1930). Similar to Chapter 2, we found that the initial genetic variance (σ^2_g) has a strong influence on the rate of evolution, resulting in an increased chance of survival (Figure A1). This is illustrated by a 40% increase in the proportion of successful founder populations (out of 1000 replicates) between those that cannot evolve (null model with no genetic variance) and simulated populations that undergo recombination and mutation with $\sigma^2_g = 0.25$. Comparing the three model types provides further evidence of how mutation and recombination influence genetic variation and affect the evolutionary processes in overcoming Allee effects. The light grey solid trend-line indicates the null model with initial genetic variation. Because variation introduces both well adapted and maladapted individuals around the mean phenotype, it is clear that a wider spread will increase the likelihood for evolutionary rescue. The darker grey long dashed line shows that with added mutation (given in Table 1), more variation is introduced and increases the proportion of successes. The black short dashed line demonstrates that random recombination can effectively discard the excess of deleterious alleles (Gardner and Kalinka 2006) contributed by increased initial variation and that accumulates with mutation, increasing mean fitness and population growth.

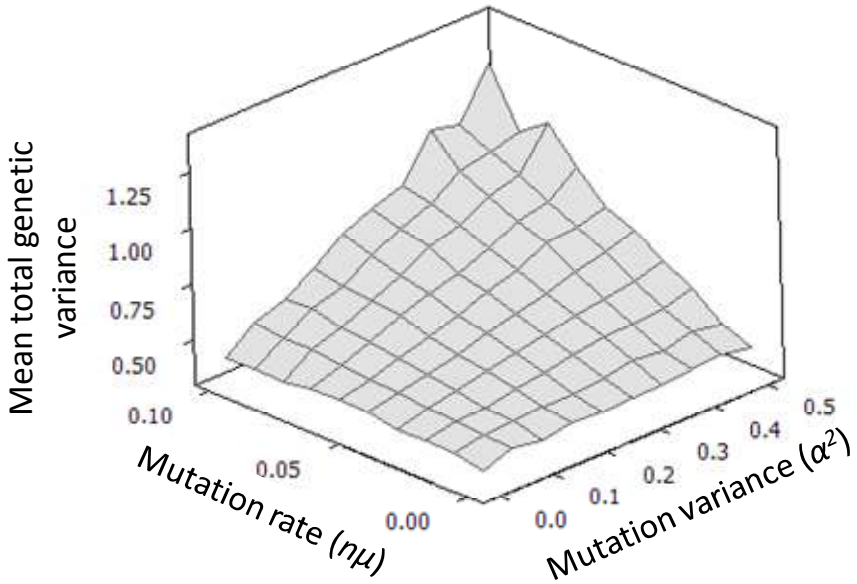
Figure A1: The proportion of successful populations of 1000 replicates according to the amount of initial genetic variance (varied from 0 to 0.25 incremented by 0.01).



Appendix B: Mutation rate and magnitude

The default values for mutation rate and magnitude (i.e., variance; Table 1) based on previous models (Burger and Lynch 1995; Holt et al 2003) have a relatively small overall effect on genetic variance and evolutionary rescue. Figure B2 shows the impact of varying the mutation rate and magnitude on the mean total additive genetic variance of successful populations after recovery (out of 1000 replicates). The initial additive genetic variance in the population is 0.5 and will fluctuate randomly with mutation events. When evolutionary rescue occurs, it is primarily due to initial genetic variance, since mutation cannot introduce enough variation early enough (within biologically reasonable values of mutation rate and magnitude) in the ecological timescale prior to extinction or growth to matter since selection acts most strongly early on.

Figure B2: Sensitivity of the mean total genetic variance (1000 replicates) of successful populations to mutation rate and variance in the mutation only model.



Appendix C: Time and number of immigrants

Shifting the focus to the process of demographic rescue without genetic variation and evolution, Figure C3 demonstrates that the size of the immigrant population and temporal proximity to the introduction of the initial population influences the likelihood of both establishment and time to extinction. The proportion of successes is increased with the number of immigrants as long as they are introduced early enough such that the founder population is not too dispersed or depauperate and the total population size is close to or exceeds the Allee threshold. Even if the number of immigrants does not dramatically increase the total population size, additional individuals contribute to the lag phase and extend the time to extinction.

Figure C4a shows the probability of success resulting from the addition of 15 individuals at different points in time. The mean immigrant phenotypes are better adapted, equal to, or maladapted relative to the initial population. Figure C4b further indicates the implications for genetic rescue based on the mean phenotype of the immigrants and genetic processes contributing to genetic variation. In this case, even a small number of immigrants (i.e., 5) where there is little demographic effect can provide the opportunity for adaptive evolution in population recovery. It should be noted that because of number of simulations presented in this figure, we used the LOWESS method of smoothing (Cleveland 1979) over the time of immigration for clarity.

Comparison of Figure C4 with Figure C3 demonstrates the additional contribution that genetic variation has on population success with evolution. For each model type in Figure C4, the original founder population and immigrant populations were initialized with expected genetic variance given in Table 1. Hence, the proportion of success

increases with adaptive evolution (null model with mean phenotype 25, light grey long dashed line Figure C4a versus dark grey short dashed line Figure C3 for 15 immigrants). A dramatic effect is observed with the introduction of five immigrants. Figure C4b shows that with added variation (in both the founder and immigrant populations), success increases compared to the low proportion of successes in Figure C3 (grey long dashed line). Even with the introduction of maladapted immigrants, success is still enhanced due to evolutionary rescue in the founder population when the five immigrants are rapidly purged from the population (the negative effect of maladapted immigrants is more pronounced with more individuals in Figure C4a). However, five individuals can positively affect the mean phenotype when well-adapted, resulting in genetic rescue.

Figure C3: The proportion of successes and the average time to extinction based on the timing and size of an immigrant population upon introduction.

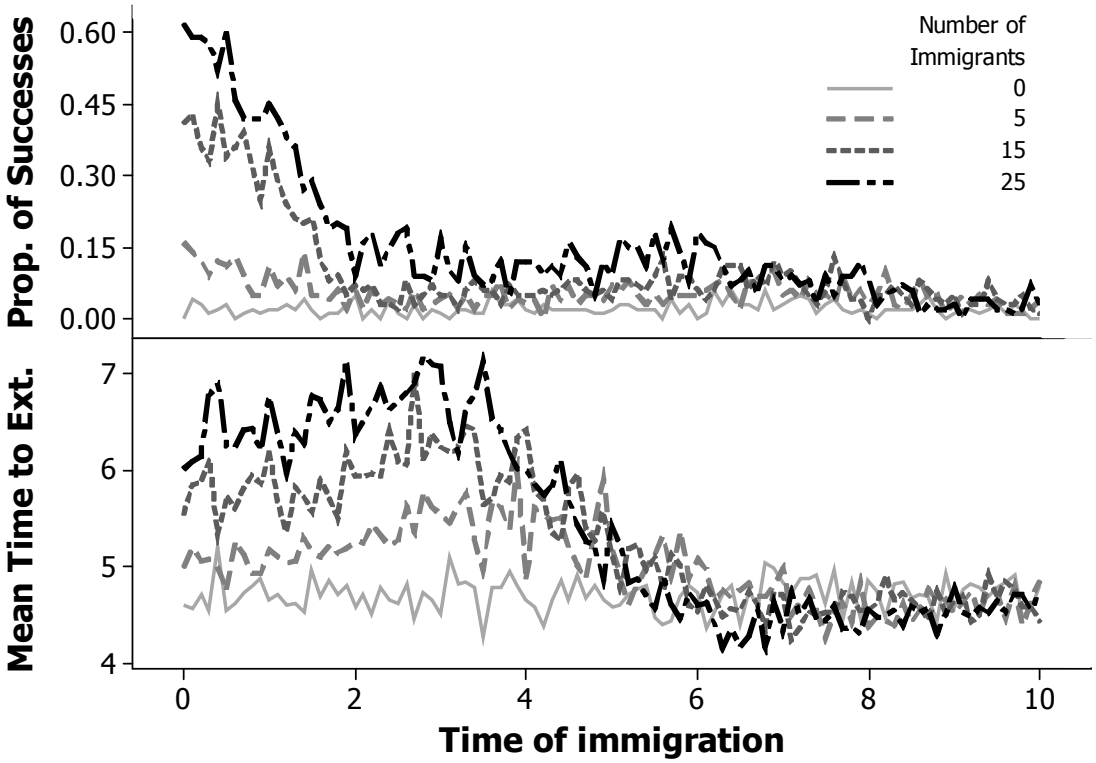
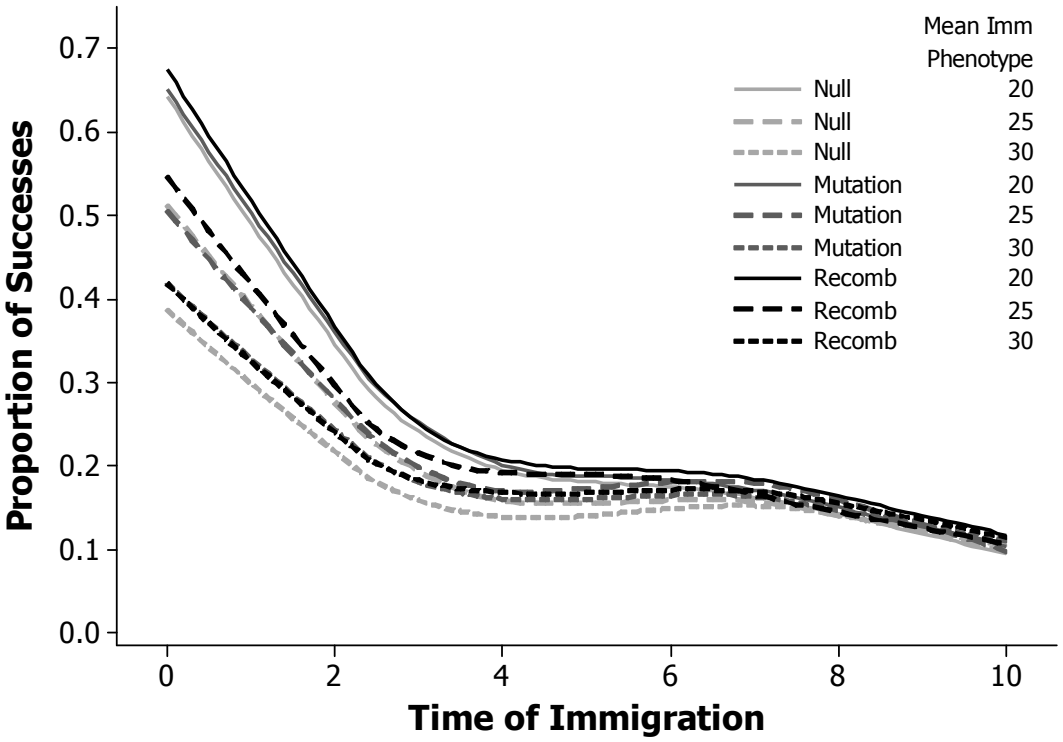
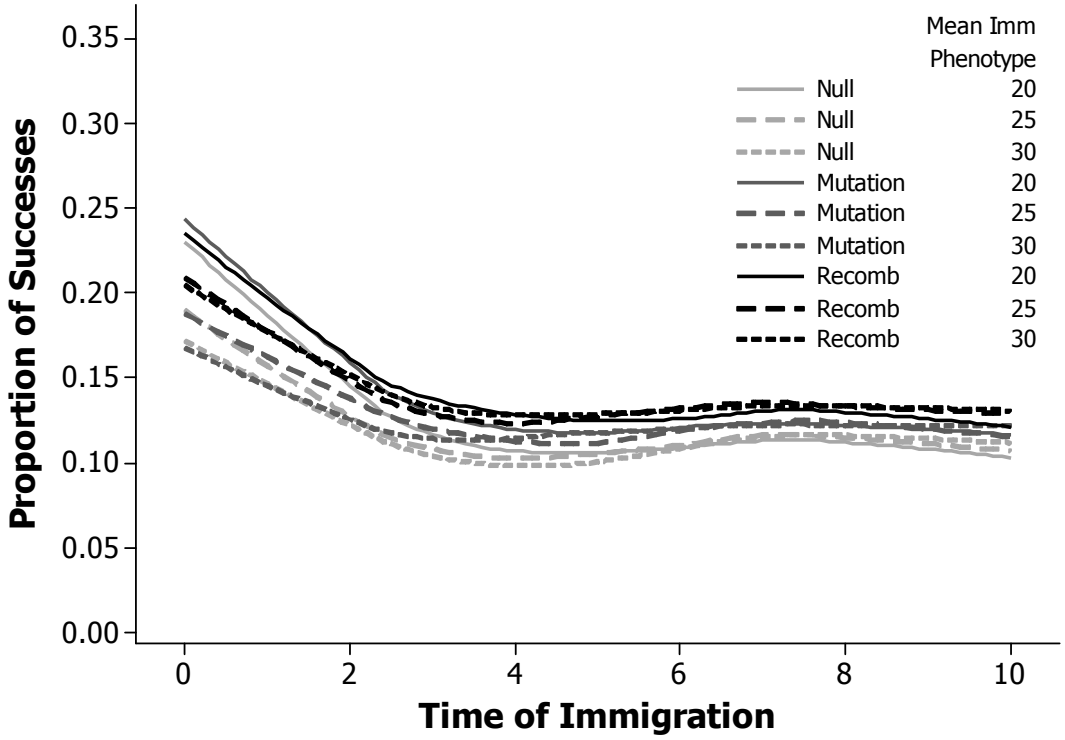


Figure C4: The proportion of successes based on the timing and mean phenotype of the immigrant population upon introduction for each model type. The immigrant population size is 15 in (a) and 5 in (b). Trend-lines were generated with LOWESS smoothing across time of immigration (with degree 0.5 with 2 iterations).

(a)



(b)


Mean Imm
Phenotype
Null 20
Null 25
Null 30
Mutation 20
Mutation 25
Mutation 30
Recomb 20
Recomb 25
Recomb 30
Proportion of Successes
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
2
4
6
8
10
Time of Immigration

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CHAPTER 5

General conclusions and future directions

For this dissertation I developed and explored an analytical model and computer simulations to address the ecological and evolutionary consequences of strong Allee effects in small founder populations of invasive species. The overall framework that I used for representing positive density dependence is heuristically robust for informing ecological theory. During the inception of this project, part of the inspiration for adopting this type of model was for its applicability across biological systems, such as forecasting invasion risk of introduced nonindigenous freshwater and marine species through ballast water discharge (Drake et al., 2005; Drury et al., 2007). In realizing some of the limitations of this previous work, however, I started down the path of this dissertation. And with this approach, I have been asking whether founder populations destined for extinction have the potential to overcome this expectation.

Beginning with the deterministic reaction-diffusion model, after working out the ecological dynamics, I began to consider whether evolution could interact with those rapid timescales. With a quantitative genetic approach to develop conditions and explore the possibility of rapid evolution rescuing the population from going extinct, the results show recovery is not only dependent upon initial density, occupied spatial extent, and demographic parameters (i.e., reproductive rate and diffusion coefficient), but that the initial genetic variance is crucial to the rate at which this occurs in the race against extinction.

To enhance both complexity and realism of the biological framework, I developed an individual-based simulation (Chapter 3). In analyzing this model, I discovered interesting ecological consequences of component Allee effects. Essentially, due to endogenous spatial structure both initially and emerging from limited dispersal, it is evident that component Allee effects vary based on individual circumstances (i.e., local interactions) and do not necessarily scale up to demographic Allee effects allowing the population to persist (Chapter 3). Incorporating evolutionary dynamics and immigration into the individual-based model (Chapter 4), I have shown that because of the pace of ecological processes and stochastic effects, evolutionary rescue is a relatively rare occurrence. As in Chapter 2, the likelihood of this happening depends primarily on the initial genetic variance and can be enhanced by recombination more so than mutation. Thus, the main source of rescue was through additional migrants that not only demographically suppressed Allee effects, but helped delay extinction during which evolution could occur.

Based on the literature review in Chapter 1, the results that I have presented throughout this dissertation are conceptually relevant and contribute to general ecological and evolutionary theory. The natural future direction of my research program is to explicitly address specific mechanisms and the associated individual-level fitness trade-offs within low density populations that generate component Allee effects. Taking into account the interactions of multiple components of individual fitness will provide a framework to better assess the emergence of Allee effects from the perspective of life history evolution. The goal will be to explicitly incorporate costs and benefits associated with aggregation formation versus increased dispersal on individual fitness, while

accounting for the exogenous environment as well. Recent work has developed optimization methods for the interaction between resource allocation and behavioral and morphological defenses (Steiner & Pfeiffer 2007; Cressler et al. 2010). This project will be developed in a similar vein, but with a focus on inducible mechanisms that optimize fitness at low density.

With the general concepts addressed throughout this dissertation, it is clear that an individual within a small population is relieved of some pressures (e.g., competition for resources), but is faced with others (e.g., finding a mate). Conflicting demands on individuals can develop different behavioral strategies, but how and if they evolve is unclear (Nowak et al. 2010). To enable a better understanding of the underlying mechanisms that have evolved in response to the selection pressures that arise at low density, I will focus on multiple interacting traits based on ecological, physiological, and demographic factors. I plan to initially address these questions by extending the spatially explicit individual-based simulation developed for this dissertation with additional components for various dimensions of individual condition (e.g., age, size, abiotic and biotic environment, energy level) and genetic disposition. The crux of this project will be the development of the eco-physiological functional response equations to determine how energy is allocated and the relative time spent dispersing, foraging, searching for mates and reproducing, and predator defense and avoidance. This approach has promise in offering more insight beyond the conceptual conclusions presented here.

Accounting for complex genetic interactions is another natural extension of this work; to provide more insight on the genetic and evolutionary consequences of small populations. In addition to explicitly modeling the factors that give rise to reproductive

and survival component Allee effects, incorporating gene regulation networks can add an interesting dimension to our understanding of genetic Allee effects (e.g., sampling effect, genetic drift, and inbreeding). Non-linearities in the genetic architecture have the potential to counteract some of these effects whereby dismantling co-adapted gene complexes when the population dynamic suddenly changes may further enhance evolvability (Brodie 2000; Lee and Gelembiuk 2008). Based on the assumptions of the wiring or complexity of a gene regulation network, the sensitivity of gene complexes to mutation and recombination may significantly influence the amount of additive genetic variation for fitness related traits (Kimbrell and Holt 2007).

Not only can dispersal or aggregation lead to multiple ecological effects as demonstrated in Chapter 3, but it can also impact gene flow and the genetic mechanisms of group formation (Nowak et al. 2010). Thus, in addition to the ecological consequences that may emerge from an extended model, including multiple levels of complexity can reveal the possibility of multifarious effects on behavior and evolutionarily labile responses. Overall, the synthetic approach of this future research can further contribute to theory in population biology and evolutionary ecology, while influencing decisions for the management of small populations... while resting soundly on the solid foundation presented in this dissertation.

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