

SYNTHESIS

Newly rare or newly common: evolutionary feedbacks through changes in population density and relative species abundance, and their management implications

Richard A. Lankau^{1,2} and Sharon Y. Strauss^{1,2}

1 Illinois Natural History Survey, University of Illinois, Urbana-Champaign, IL, USA

2 Department of Evolution and Ecology, UC Davis, Davis, CA, USA

Keywords

adaptation, community ecology, conservation biology, natural selection and contemporary evolution, population ecology, species interactions, wildlife management.

Correspondence

Richard A. Lankau, Illinois Natural History Survey, University of Illinois, Urbana-Champaign, IL, USA.
Tel.: (217) 419-4113; fax: (706) 542-1805;
e-mail: ralankau@illinois.edu

Received: 14 November 2010

Accepted: 18 November 2010

doi:10.1111/j.1752-4571.2010.00173.x

Abstract

Environmental management typically seeks to increase or maintain the population sizes of desirable species and to decrease population sizes of undesirable pests, pathogens, or invaders. With changes in population size come long-recognized changes in ecological processes that act in a density-dependent fashion. While the ecological effects of density dependence have been well studied, the evolutionary effects of changes in population size, via changes in ecological interactions with community members, are underappreciated. Here, we provide examples of changing selective pressures on, or evolution in, species as a result of changes in either density of conspecifics or changes in the frequency of heterospecific versus conspecific interactions. We also discuss the management implications of such evolutionary responses in species that have experienced rapid increases or decreases in density caused by human actions.

Introduction

Many of the major issues in environmental and conservation management concern the manipulation of population abundance. For desirable species, the management goal is generally to increase or maintain the population at a size that is resilient to environmental stressors or to stochastic events. For undesirable species, such as invaders, pests, or pathogens, the goal is often to decrease the population size, ideally to extinction. Changes in the population size of a species affect two separate, but related, ecological properties: (i) processes that act in a density-dependent fashion, and (ii) processes that depend on the frequency of interactions that a species has with heterospecifics versus conspecifics. Both changes in density and changes in relative frequency of interactions can lead to cascading changes in other species. Thus, it has been increasingly recognized that management may gain from an understanding of the community context of numerical changes (Root et al. 2003; Early and Thomas 2007).

Along with numerical changes in species' abundances, rapid environmental changes driven by human activities (including harvesting, development, agriculture, and species introductions) are exerting new and strong selective pressures on wild populations; these populations are responding both plastically and evolutionarily with rapid changes in trait distributions (Tabashnik 1994; Peck 2001; Hendry et al. 2008; Darimont et al. 2009). Some of the clearest examples of evolutionary trait changes in response to human activities are changes in body size and life history in overharvested marine fisheries, as well as the evolution of resistance to pesticides and antibiotics in arthropod pests and bacteria, respectively. The selective impacts of humans are exceedingly strong and consistent (Hendry et al. 2008) and will thus often result in predictable evolutionary responses by populations. For example, resistance has evolved multiple times independently to many different chemical pesticides (Gassmann et al. 2009), and in many species of insect pest [e.g., (Alon et al. 2006; Williamson et al. 1996)]. Moreover, the rate of phenotypic change in populations is often proportional

to the strength of selection—for instance, the rate of phenotypic change in body size and life history traits of 37 marine fisheries were directly proportional to harvest intensity (Sharpe and Hendry 2009). Though we might be able to predict how populations may evolve in response to these kinds of anthropogenic selective pressures, *whether* populations can evolve, and the mode and tempo of the genetic response to these selection pressures is much less predictable. The mechanisms and traits underlying adaptation may vary from population to population, depending on the genetic variation and genetic architecture present in that population.

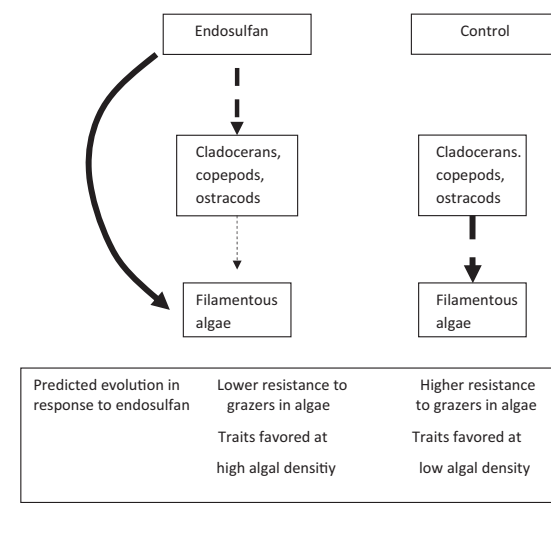
In contrast to strong sources of anthropogenic selection like biocides and overharvesting, other sources of anthropogenic impacts or natural resource management schemes are likely to have more complex, less predictable selective effects on populations and communities. This unpredictability likely arises for several reasons: (i) selection from an environmental change or management scheme may be of similar magnitude as that of other selective pressures experienced by a population, in which case conflicting selection, correlated traits, and genetic architecture may make predicting evolutionary responses more difficult (e.g., Bell 2010) and (ii) most environmental changes affect more than one species in a community. In this case, these complex selective effects will be integrated across both direct effects on a species and the indirect effects resulting from changes in other species (see Box 1 for one example and the predicted nonintuitive evolutionary response).

Most management actions are aimed at manipulating the abundance of specific populations, and these actions take place within the community context of the target species. Changing population sizes of one species will often result in correlated changes in a suite of associated species. Attention to evolutionary change has focused primarily on single population responses to schemes like harvesting or marine reserves, or to an environmental change, like rising temperature. However, we argue that much of selection, and subsequent evolutionary response, occurs in the complex context of natural communities (Antonovics 1992; Haloin and Strauss 2008; Lau 2006; Lankau 2007; Strauss and Irwin 2004). Managers and policy makers must recognize that not only may there be evolution in a managed population owing to direct selection on traits, but there will often also be indirect evolutionary consequences of a given environmental change or management action mediated by other community members. An example of complex effects of pest management ramifying through the community entails use of Malathion, a broad spectrum insecticide employed throughout the world to reduce insect pests. Malathion at low concentrations has minimal effects on leopard frogs (*Rana pipiens*) and wood frogs (*Rana sylvatica*) in classic labora-

Box 1. Unpredictable selection in complex communities.

Selection from environmental change in a community context may have unpredictable outcomes. Adding endosulfan on its own to algae reduced algal growth. However, adding endosulfan in the context of the full ecological community actually promoted algal growth through its indirect effects (Barry and Logan 1998). Endosulfan kills most ostracods, copepods and a cladoceran, grazers on algae. By reducing herbivore populations dramatically, endosulfan caused a bloom in filamentous algae (Barry and Logan 1998). Thus, while the direct effects of endosulfan on algae might be negative, the net effects on algae via the community response to endosulfan are positive. As defenses against herbivores in many plants are costly (e.g., Bergelson and Purrington 1996), we predict that once algae are released from predation, selection will favor algae that invest less in defense and that are thus stronger intraspecific competitors. Thus, a short-term evolutionary effect of endosulfan pollution could be the evolution of decreased resistance to grazers by algae. Management decisions that rely on simplified tests of strategies might miss the rich ecological context in which organisms live and thus find unintended ecological and evolutionary effects of the strategy.

In this figure, solid lines indicate positive effects and dashed lines negative effects; the thickness of the line indicates the strength of the effect,



tory toxicity assays (Relyea and Diecks 2008). However, the application of Malathion in a more species-rich pond mesocosm, in combination with realistic pond drying regimes, was lethal to the longer-lived leopard frog, *R. pipiens* (Relyea and Diecks 2008). In a nutshell, Malathion killed most of the zooplankton species, and loss of zooplankton caused a bloom of the phytoplankton, released from zooplankton predation. The phytoplankton bloom reduced light levels in the pond, and thus reduced the growth of periphyton, substrate-growing algae that are the food source of these tadpoles. Larger frogs like *R. pipiens* did not obtain adequate food before the pond

dried. Thus, while wood frogs were not so affected by complex community-based effects of Malathion, leopard frogs were very vulnerable. A possible evolutionary response to Malathion application in leopard frogs might be earlier maturation at smaller sizes. No measurements were made to quantify the response to selection in these frogs, but we argue that nonintuitive evolutionary responses to pest management (e.g., Malathion application to crops causes smaller frogs) may arise via the cascading effects of changing population size in many kinds of communities.

Below, we provide specific examples in which the density of populations alters the direction of selection on traits, concentrating our examples from field studies. There is a large literature on density-dependent ecological effects in the field; there is a small but growing literature on the subsequent evolutionary consequences of changes in population density in field populations. Some of these studies are in the now-burgeoning field of eco-evolutionary feedbacks, founded by Ford, Pimentel, Chitty, and others.

Selective consequences of changing population density

Researchers have long recognized that natural selection may favor different traits at high versus low population densities. Ford and Ford (1930) and Ford (1931) were among the first to suggest the inter-relationships between genetic changes in populations and their population dynamics. These ideas were elaborated on by others, notably Pimentel (1968) and Chitty (1967) to explain population cycles and stability. Their ideas were that individuals within populations of disparate density experience different selective pressures and express different traits; this thesis has a rich history in both theoretical and empirical studies (reviewed in Mueller 1997). Most empirical studies have been conducted in laboratory or greenhouse settings; though, these environments may be too simplified to detect conflicting selection present in complex natural communities (e.g., Shaw et al. 1995). Studying evolution and trait changes with density in field populations is a challenge, however, especially in the absence of experimental manipulation of densities, because population density and other factors may covary in the field. Additionally, many ecological studies of density regulation do not measure the demographic impact of density perturbations on individual life history traits, which is necessary to make evolutionary predictions (Bassar et al. 2010b). Despite these difficulties, there is evidence that genetic changes occur and populations evolve as they go through different densities in population cycles. In field studies of a population of Soay sheep, both horn and coat color polymorphisms appear to be maintained through opposing selection

pressures at low and high population densities (Moorcroft et al. 1996); the mechanisms underlying the selective value of these traits are unclear, although dark coat color is genetically linked to body size (Gratten et al. 2008), a trait well-known to respond to density (e.g., Walsh and Reznick 2008). Field studies have shown that life history traits can be under selection from density in the field (e.g., Sinclair et al. 2003). Thus, rapid changes in density of wild populations through a whole host of human-caused activities—harvesting, conservation management, species introduction, habitat loss—may have selective effects through changes in density.

We first discuss the selective effects of changing conspecific population densities in isolation. Next, we address the selective impacts of the altered interactions with other trophic levels predicted to occur with density changes. We then address how changing the *frequency* of interactions with conspecifics versus heterospecifics, a function of the relative abundance of each species, might also select for different suites of traits. Finally, we explore the potential evolutionary consequences of rapid changes in density brought about by environmental changes and management actions.

Density-dependent selection driven by within-population dynamics

Life history traits respond to intraspecific density—*r*- and *K*-selection revisited

The role of population density in the evolution of life history traits has a long and contentious scientific history, which we will only address briefly here. Chitty (1967), Pimentel (1968) and MacArthur and Wilson (1967) suggested that selection would tend to favor traits that increase *r*, the intrinsic population growth rate when the population is at low density relative to its resource base. Moreover, different traits may optimize fitness when the population is at high density near *K*, the carrying capacity. In short, at low densities far from *K*, genotypes with a higher intrinsic (density-independent) population growth rate will increase faster than those with lower *r* values. However, when densities are at or near *K*, the favored genotypes will be those that use resources most efficiently, in other words have the highest genotype-specific *K* value. If the phenotypic traits that underlie a high intrinsic growth rate trade-off with those that lead to efficient use of limiting resources, then density fluctuations should lead to shifting selection pressures on populations. This suggestion inspired many decades of research aimed at predicting the traits that drive high *r* versus those that drive high *K*. Commonly cited examples of 'r-selected traits' include early reproduction, short life spans, and reduced investment to maintenance functions

like immune systems, whereas 'K-selected traits' are often the inverse (Boyce 1984; Mueller 1997; Reznick et al. 2002; Einum et al. 2008). As a field example, killifish from low-density, predator-rich environments reproduce earlier and are better adapted to exploiting high resource levels, while those from high-density, predator-free areas appear adapted to chronically low resource levels (Walsh and Reznick 2008). Additionally, when raised in a common environment, individuals from an invasive *Spartina alterniflora* population that had recently taken over open habitat on the west coast had earlier reproduction and higher reproductive effort, but also earlier mortality, than individuals from high-density native east coast populations (Davis 2005).

However, there are many examples where the simple predictions of this theory do not hold, leading some researchers to conclude that the theory has out-lived its usefulness, preferring to focus on the role of age-specific mortality rather than density as the driving selective force shaping life history (Stearns 1977). Mueller (1997) notes that despite the fact that it has been difficult to find generalizable trait differences between high- and low-density species (the vast majority of these studies involve comparisons between species, rather than genotypes), the most basic prediction of MacArthur and Wilson's initial theory is still sound. Numerous studies in controlled settings, for example with *Drosophila melanogaster* populations in laboratories, or with *Musca* blowflies and their *Nasonia* parasitoids, have confirmed these trade-offs in traits at low and high densities (Pimentel 1968; Mueller et al. 1991). Moreover, the blowfly experiments also show that evolution of resistance in the fly host populations to the wasp parasitoid alters the carrying capacity of the environment for both flies and wasps, leading to eco-evolutionary feedbacks. The difficulty comes in determining what traits underlie r and K in complex natural situations (Reznick et al. 2002). An additional complexity arises from selection on traits favored in competition at high density; selection on traits involved in interference competition (such as territoriality) may lead to reduced population level K, counter to the original prediction of the theory.

In natural conditions, changes in population density do not occur independently of the rest of the interacting community, and these community interactions may be the strongest determinant of which genotypes or traits confer the highest fitness at low or high density. In the following sections, we explore specifically how competitive interactions in a community context, among both conspecifics and heterospecifics, as well as interactions with other trophic levels, can lead to density-dependent selection pressures. We argue that some of these selective pressures are not easily predicted from the r- and K-selection framework.

Self-thinning in populations may exert strong selection on traits

Self-thinning is a density-dependent process that occurs in many field populations but has been given little attention as a source of selection. While r- and K-selection theory (and studies of density-dependent selection in general) tends to focus on comparisons of high- and low-density populations, for many species the density of a population is dynamic, even within a single generation. Self-thinning is the reduction in intraspecific density of organisms in early life stages because many more young are born than can be supported in a given area. This phenomenon is reported for mussels, other invertebrates, fish, and many plant species (e.g., Brichette et al. 2001). In California grasslands, there are between 60 000 and 300 000 grass seeds per m² at the start of the growing season, and over 90% (54 000–270 000) of these seeds germinate once winter rains begin. Of these, approximately 50% die in the first few weeks and thinning continues to adult plant densities ranging from 8000 to 20 000 individuals per m² (Heady 1958; Bartolome 1979, Young et al. 1981, as summarized in Eviner and Firestone 2007). Thus, from these figures, one can estimate that 97–63% of germinating seeds die. While these annual grasses may be extreme cases of self-thinning, in a study of invasive yellow starthistle (*Centaurea solstitialis*), Garren and Strauss (2009) found that only 5% of seeds germinating in experimentally cleared areas became reproductive adult plants (Fig. 1); 5% is probably an overestimate of survivorship, as many more seeds were deposited in uncleared nonexperimental areas where there was only approximately 1% survival from seed to adult. Similar dramatic self-thinning processes occur in settling mollusk larvae and fish hatchling populations (e.g., Brichette et al. 2001; Lobon-Cervia 2008).

Despite the fact that there is huge mortality in the transition from hatchling, larva or seed to adult, there have been almost no studies examining whether selection during the self-thinning process affects traits of reproducing adults. A descriptive longitudinal study comparing genetic variation in the seed bank, seedling, and adult stages of *Atriplex tatarica* showed that at seven loci, rare alleles were more common in adult populations than in seed and seedling populations (Mandak et al. 2006a). In addition, reproducing plant populations had greater levels of heterozygosity, associated with greater vigor in this species, than did seed or seedling populations (Mandak et al. 2006b). Finally, the greatest changes in allele frequencies occurred between seedling and mature plant stages; the authors attribute these changes to selection through the self-thinning process. In mussels, there appears to be genetic variation for both intraspecific

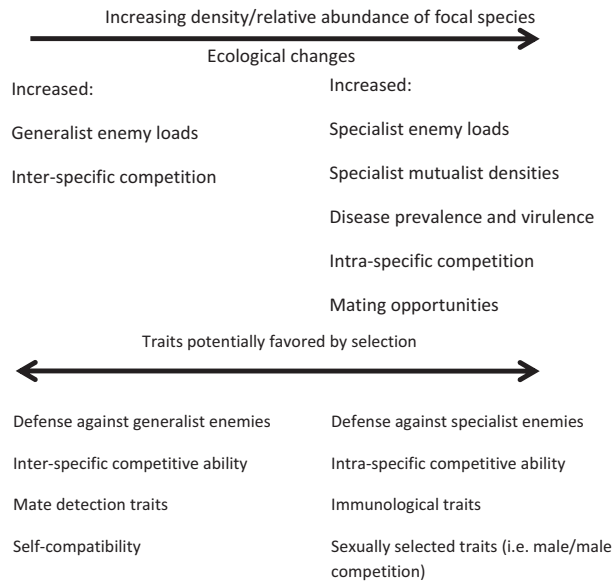


Figure 1 Changes in a focal species' abundance predictably affect interactions with other species. These interactions, in turn, may result in shifting selection pressures on a number of traits as the abundance of a focal species changes.

competitive ability and reduction in the impact of competition on mussel growth; both of these attributes have been suggested as traits for artificial selection to increase yields of mussels (Brichette et al. 2001). Even nonseeding animals may experience selection via self-thinning. Self-thinning dynamics occur in grasshopper and other mobile animal populations (Begon et al. 1986). Moreover, while there was no correlation with body size, Rose et al. (1998) found that cohorts of red deer that underwent high initial mortality subsequently had greater adult survivorship than cohorts not subjected to high density-related selection early in life.

Management strategies that ignore selection over these life stages may have unintended consequences. For example, introducing predispersal biological control agents that dramatically reduce seed density of pest plants could also reduce the importance of self-thinning processes as sources of selection in determining the traits of reproducing adults (Fig. 2 and described later). Increasingly, trait distributions of populations are being shown to have great impacts on ecosystems, and trait values of individuals sometimes have even greater impacts than population density in affecting ecosystem properties (e.g., Bassar et al. 2010a,b).

Mating system traits may be under opposing selection at low and high intraspecific density

In animals, population density may also alter selection on mating systems and sexual aggression traits (Emlen and

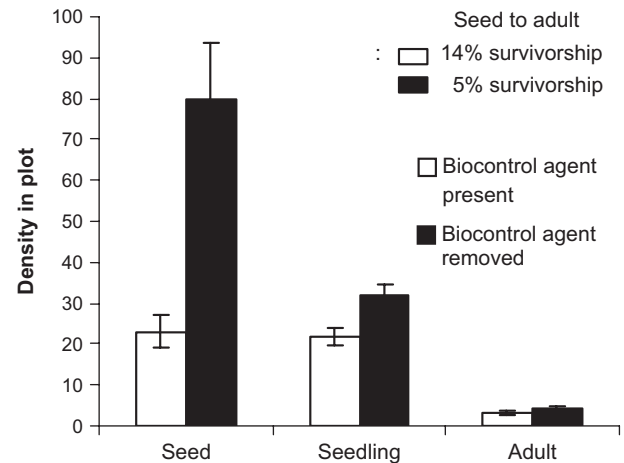


Figure 2 The density of seeds, seedlings, and adults of yellow star-thistle (*Centaurea solstitialis*) in plots where weevil and fly biological control agents were experimentally removed and in control plots. Although seed predators reduced the seed deposition into plots by more than 50%, self-thinning in plots resulted in equal adult plant densities in plots, regardless of seed inputs. More data and experimental protocol can be found in the study by Garren and Strauss 2009.

Oring 1977; Maher and Lott 2000; Kwiatkowski and Sullivan 2002; Horiuchi 2008; Knell 2009). At low densities, mate detection traits may be of paramount importance, while traits involved in mate competition or territory defense may be under weak selection because conspecific encounter rates will be low (Maher and Lott 2000; Knell 2009). At intermediate densities, territory defense and mate guarding may be favored, and finally at very high densities, males may be selected to forgo direct competition with other males (because of the high cost of frequent encounters) and instead follow a scramble or lekking strategy (Emlen and Oring 1977; Knell 2009). In plants, changes in population density can affect mating system evolution via changes in the abundance and diversity of pollinators. At high densities, an abundance of pollen donors and pollinators may select for increased self-incompatibility, as this can help avoid the negative effects of inbreeding (Moeller and Geber 2005; Morgan et al. 2005; Mimura and Aitken 2007). However, at low densities, self-incompatibility systems may be costly because individuals will frequently fail to receive pollen from other individuals. In this situation, a higher rate of selfing would be selectively favored for reproductive assurance, as the benefit of increased fecundity would override any costs of inbreeding depression (Davis 2005). Thus, a threatened plant species that was formerly abundant and is currently rare (i.e., a newly rare species) may be more pollen limited than a rare species that has evolved traits suited to consistently low densities

(see Eckert et al. 2010 for a review of effects of anthropogenic disturbance on plant mating systems).

Selection imposed by density-dependent changes in other trophic levels

As we have seen, density-dependent selection can result from interactions among individuals of the focal species. However, placing density-dependent selection in the context of multispecies communities provides a wealth of examples in which fitness-affecting interactions with other species are density dependent. While there is, again, a huge body of work on the ecological implications of density dependence in community composition, the evolutionary implications are understudied, except in theory (e.g., Abrams 2009; Loeuille 2010).

Density-dependent effects on prey populations

A predator population that increases in density will likely have a greater impact on its preferred prey. If the preferred prey population declines enough, selection may favor predator genotypes that can utilize alternative prey species. One clear example of this comes from changes in alewife densities in lakes caused by disruption of migratory behavior. Anadromous populations of alewife feed selectively on large-bodied zooplankton as young of the year, but then migrate to oceans in the fall, allowing the large-bodied zooplankton species to recover in time for the next season's hatch (Post and Palkovacs 2009). In lakes cut off from the ocean by dams, alewife populations are resident year-round. This increase in density in the fall and winter months drives down the populations of large-bodied zooplankton, favoring alewife individuals able to feed effectively on smaller zooplankton species. Over time, changes in density and food availability have led to evolutionary changes in alewife morphology (smaller gapes and narrower spacing between gill rakers) that facilitate feeding on the smaller species (Palkovacs and Post 2008, Palkovacs and Post 2009).

Density-dependent relationships with enemies

Changes in the density of a species may lead to increases in attack rates from specialized consumers that forage or use hosts in a density-dependent manner. For instance, damage from specialist herbivores often increases with increasing abundance of their host plant species. (e.g., Root 1973). Specialist herbivores are less likely to immigrate to, and more likely to emigrate from, patches with a low density of host plants. Thus, at low density, a plant species is likely to face a higher proportion of damage from generalist versus specialist

herbivores, while at high density, this situation would be reversed. The selective effects of such density-dependent effects are also apparent. The traits that provide resistance to specialist herbivores typically differ from those involved in resistance to generalist herbivores (Giamoustaris and Mithen 1995; van der Meijden 1996; Lankau 2007). Co-evolved specialist herbivores often have effective countermeasures to chemical defenses (Nitao 1989; Stermitz et al. 1989; Kelly and Scriber 1993; Siemens and Mitchell-Olds 1996; van der Meijden 1996). Thus, when plants are at low densities (and consequently experiencing a high ratio of generalist versus specialist herbivory), selection may favor higher concentrations of defensive chemicals. At high abundance of the host, however, these chemicals may be less valuable, if most of the damage comes from specialized herbivores that are adapted to plant defenses (Agrawal et al. 2006). High specialist loads typical of high-density populations may thus select for structural defenses or tolerance to herbivory to which the specialists cannot evolve direct resistance (Clauss et al. 2006). Experimental removal of specialist and generalist herbivores of *Brassica nigra* shows that herbivore communities of only generalists selected for high levels of the chemical defense sinigrin; the presence of specialists negated that selective effect to yield no net selection on sinigrin when both specialists and generalists were present (Lankau 2007). Moreover, when grown with a conspecific neighbor and the full complement of herbivores, selection favored lower sinigrin levels (Lankau and Strauss 2008). However, when grown with a heterospecific neighbor and these same herbivores, selection favored higher levels of the chemical defense. This pattern occurred primarily because the specialist herbivores behaved differently in the two situations, being selective feeders when there were several *B. nigra* plants present, but nonselective when there was only one *B. nigra* individual (Lankau and Strauss 2008).

Similarly, infectious diseases often also track host population size and thus may impose density-dependent selection. In order for a disease to maintain an endemic infection, there must be a reliable source of susceptible hosts and high enough transmission rates from infected to susceptible individuals (Burdon et al. 1995; Ericson et al. 1999). Low relative abundance of the host can reduce disease persistence by reducing the total number of susceptible hosts (a density-dependent effect termed susceptible host regulation). For instance, *Lolium perenne* grass cultivars that differed in resistance to a rust fungus varied in their infection rates in plots with high host density; the same cultivars showed no differences in infection rates when grown in low-density plots, where infection rates were overall much lower (Roscher et al. 2007). Thus,

the difference in densities among these plots alters selection on disease resistance in *L. perenne*.

Virulence of the pathogen is also a trait that evolves via a trade-off between transmission and host exploitation, and by the degree of within-host competition between disease strains (Ewald 1994). At high host densities, disease fitness may be greatest in strains that quickly build up high populations within hosts and transmit themselves effectively to the next host (i.e., selection for increased virulence is expected to evolve with frequent host encounters that lead to both higher transmission rates and a greater likelihood of multiple infections) (Frank 1996). On the other hand, low transmission rates in low-density host species select for less virulent disease; decreased virulence prolongs the life of the host and thus the time period for successful transmission between hosts. Moreover, the evolving virulence of local disease strains can, in turn, have a strong impact on the evolution of resistance traits in host species (Thrall and Burdon 2003). Here, host and disease evolution are mediated by frequency of encounter.

For both plants and animals, there are many other examples of density-dependent attack from enemies; generally, if there are energetic or ecological costs of resistance to such enemies, then we predict that high-density populations should be consistently selected to be more resistant to enemies and that low-density populations should be selected to be less resistant.

Density-dependent relationships with mutualists

While a high density of conspecifics may decrease individual fitness because of the build up of specialist consumers, individuals may benefit from a similar build up of specialist mutualists. Just like specialist herbivores and predators, specialist pollinators and seed dispersers may preferentially forage in patches with a high density of their host (Kolb 2008; Sober et al. 2009). Specialized pollinators tend to be more effective from the plant's perspective as less pollen is wasted on other plant species, and less interspecific pollen is transferred to their flowers (Johnson and Steiner 2000; Fenster et al. 2004; Larsson 2005). Plant species at low relative abundance may thus be selected to specialize in their pollinator interactions—otherwise they will receive high levels of interspecific pollen from more common plant species (Sargent and Otto 2006). Castillo et al. (2002) showed both positive density and positive frequency-dependent selection on floral rewards in *Begonia gracilis*. Pollinator visitation and fruit set were almost perfectly correlated in this study ($r = 0.94$). When flowers were abundant, pollinators discriminated among flowers, going preferentially to those that were the most rewarding; pollinators did not discriminate between flowers with different

reward amounts when flowers were scarce. Pollinators also foraged at high-reward flowers at greater rates than expected when high-reward plants were at high frequency, and at lower rates than expected when they were rare. Thus, in this system, as in others (e.g., Moeller and Geber 2005; Morgan et al. 2005; Mimura and Aitken 2007), selection on reward traits will depend both on how abundant flowers are and on the frequency with which pollinators encounter other flowers with different rewards.

Selective consequences of changes in the relative frequency of interactions with conspecifics versus heterospecifics

An overlooked attribute of density-dependent selection regimes is not only selection arising from encounter rates between conspecifics but also selection from encounter rates with heterospecifics. The relative abundance of a given species with respect to other species may be as important a property as the absolute density of that species in predicting both ecological and evolutionary outcomes. At high relative abundance, individuals will frequently interact with conspecifics, while at low relative abundance, they will be much more likely to interact with individuals of other species. The ecological effects of changing relative abundance of community members have been explored extensively (e.g. the Janzen–Connell hypothesis). In applied settings, they have been exploited to manage agricultural systems, for example, where adding species diversity to fields, through intercrops, hedgerows, or acceptable levels of weed growth, can reduce damage from crop specialist pests (e.g. Root 1973; Andow 1991). The *evolutionary* effects of these shifts in relative abundance have been largely ignored, however. Again, because species management schemes for either rare or invasive species focus on altering abundance of species, we may see evolutionary changes accompanying changing frequency of interactions between conspecifics and heterospecifics.

Traits that are favored at high densities of conspecifics and under frequent intraspecific interactions may not be the same as those favored when species are interacting primarily with heterospecifics (Table 1 provides a few examples). Below, we describe in more detail some specific cases from field experiments in which the frequency of interactions between heterospecifics and conspecifics alters selection on traits.

Traits conferring greater intraspecific competitive ability may trade off with traits favored under interspecific competition

A direct test of whether there are evolutionary trade-offs based on competitor identity (heterospecific versus

Table 1. Some examples of trade-offs between traits favored at high versus low frequency of interactions with heterospecifics or trade-offs between traits favored at high versus low conspecific population densities.

Species	Common name	Trait with respect to interspecific interaction	Mechanism	References
<i>Rivulus hartii</i>	Trinidad killifish	Life history traits	Fish are locally adapted to both direct effects of predators and indirect effects mediated through density/resource availability	Walsh and Reznick (2008)
<i>Anelosimus studiosus</i>	Social spiders	Aggressiveness	Nonaggressive social phenotypes tolerate higher intraspecific density and have higher resource use efficiency than asocial phenotypes, which fight more with conspecifics but are better defenders against heterospecifics	Pruitt and Riechert (2009); Pruitt et al. (2008)
<i>Nemophila menziesii</i>	Baby blue eyes	NA	Plant genotypes that have high fitness at high densities of <i>N. menziesii</i> do poorly at high densities of interspecific competitor <i>B. diandrus</i> , and vice versa	Shaw et al. (1995)
<i>Brassica nigra</i>	Black mustard	Allelopathy	More allelopathic genotypes are better interspecific, but poorer intraspecific competitors	Lankau and Strauss (2007)
<i>Alliaria petiolata</i>	Garlic mustard	Allelopathy	More allelopathic genotypes are better interspecific, but poorer intraspecific competitors	Lankau et al. (2009)
<i>Lepus americanus</i>	Snowshoe hare	Life history traits	Over 16 years of captive breeding, hare lineages collected at high-density points of population cycles had reduced reproductive rates relative to lineages collected from low-density points in cycles.	Sinclair et al. (2003)

conspecific) would be to compare the performance of genotypes across divergent selective regimes of inter- and intraspecific competition (Miller and Schemske 1990; Miller 1995; Mueller 1997). Very few such studies have been conducted, and even fewer have been conducted within the complex context of field communities. Here, we focus on examples from the field.

Shaw et al. (1995) grew genotypes from controlled crosses of native *Nemophila menziesii* along a gradient of encounter frequency with the heterospecific, *Bromus diandrus* in the field. At some sites, they found environment-dependent trade-offs between intra- and interspecific competitive ability in *N. menziesii*—that is, genotypes that did well in intraspecific competition did poorly in interspecific competition; no evidence for such trade-offs was found in comparable greenhouse studies.

Brassica nigra plants grown with heterospecific neighbors (three different species) in the field experience selection to increase their investment in sinigrin, a toxic secondary compound, while those grown with conspecific neighbors are selected to decrease their investment in the same allelochemical (Lankau and Strauss 2008). Similar patterns were observed in naturally occurring patches of black mustard that varied in percent composition of conspecifics and heterospecifics and experiments in which neighborhood (conspecific or heterospecific) was manipulated. Thus, there is conflicting selection on the sinigrin traits under intra- ver-

sus interspecific competition; these trade-offs are mediated by the effects of sinigrin on soil communities containing arbuscular mycorrhizal fungi (AMF) mutualists of heterospecifics (Lankau et al. 2010), further emphasizing the importance of evolution in a full-field community context to detect such effects. While other studies have failed to find these trade-offs in plants, few of these were conducted under natural field conditions, being greenhouse, laboratory, or agricultural field studies (e.g., Miller and Schemske 1990). Laboratory studies of *Tribolium* and *Drosophila* find evidence both for and against this trade-off in competitive ability (reviewed in Mueller 1997); the simplified conditions of these environments may also not adequately simulate selection in nature.

Evolutionary effects of frequency-dependent soil feedbacks on plants

Soil communities contain a diverse mix of mutualistic and pathogenic species, and different plant species can alter this mix over the course of their growth. Soil feedbacks occur when the presence of a plant fosters particular soil communities at its roots, and these soil communities either promote or inhibit the growth of a conspecific or heterospecific (Reinhart and Callaway 2006; Kulmatiski et al. 2008). Studies have often found that native species condition soil communities that reduce the

growth of conspecifics, implying that at high relative abundance, native plants will often face net negative interactions with their soil communities. As a corollary, individual plants are more likely to perform better in soils previously conditioned by a heterospecific. The likelihood of encountering soils conditioned by conspecifics versus heterospecifics depends on the relative abundance of these species. Again, the evolutionary consequences of this phenomenon have not generally been explored. However, one could predict that at high relative abundances, selection will favor traits that provide resistance or tolerance to these negative interactions with soil microbes (Seifert et al. 2009), while selection on these traits may be relaxed when a species is at low relative abundance.

Personality traits in animals evolve depending on the frequency of inter- and intraspecific interactions

In animals, competitive interactions between species are often behaviorally mediated, and behavioral syndromes (correlations between different behaviors, also known as animal personalities) may lead to trade-offs between the behavioral suites favored in interspecific versus intraspecific competition. For example, western bluebirds are currently expanding their range to re-establish populations in areas where they were historically extirpated because of logging and agricultural practices. When artificial nest boxes became common in the last 35–40 years, boxes were quickly colonized by mountain bluebirds, which had remained in the area at higher elevations. Western bluebirds followed thereafter, and aggressively displaced the mountain bluebird within 10 years. Thus, on the leading edge of the expansion, western bluebirds experience frequent competition with their congener, but rarely with conspecifics. However, this situation quickly changes to one with frequent conspecific interactions and fewer congeneric ones, as the mountain bluebirds are displaced. By comparing recently established and older western bluebird populations, Duckworth and Badyaev (2007) found that newly established populations had a much greater proportion of aggressive individuals. Additionally, selection analyses found that aggressiveness was strongly selected against older populations (which lacked mountain bluebirds), possibly because of the poor parental care provided by aggressive individuals (Duckworth and Badyaev 2007). Thus, behavioral traits are under opposing selection in conspecific versus heterospecific dominant populations. Similarly, heterospecific web parasites and predators are deterred by asocial, more aggressive genotypes of the social spider *Anelosimus studiosus* than by social genotypes; at high conspecific densities, however, asocial spiders are less efficient at converting prey into the next generation of spiders, owing to their high level

of aggressiveness toward conspecifics (Pruitt and Riechert 2009; Pruitt et al. 2008).

The response to selection and its ecological consequences

Up to this point, we have only discussed reasons why certain traits may face different selection pressures at high versus low population densities and/or at high versus low frequency in a community. In order for a population to show an evolutionary response to such selection, it must have sufficient heritable variation in relevant genes, and the deterministic effects of selection must overwhelm stochastic processes (i.e., genetic drift). On average, genetic variation is expected to be lower, and the role of genetic drift stronger, in low-density populations. Therefore, one might predict that the traits favored in high-density populations (such as intraspecific competitive ability or resistance to specialist consumers) would show a faster and/or stronger response to selection than traits favored at low density.

Additionally, in most of the preceding discussion, we have chosen to simplify matters by contrasting 'high' versus 'low' density situations. However, population density is a dynamic quantity, which will change over time for a given population based on biotic and abiotic conditions. Importantly, population densities may themselves change because of evolutionary changes within the population, an example of an eco-evolutionary feedback (Saccheri and Hanski 2006; Kinnison and Hairston 2007; Fussman et al. 2007). When density is controlled by extrinsic factors, populations may undergo evolutionary changes without experiencing any density changes (referred to as soft selection, Christiansen 1975). For example, in a bird population where density is controlled by the number of nest sites, inter-genotypic competition may lead to evolutionary changes in traits without increasing the size of the population (which will never exceed the number of nest sites). On the other hand, for populations far from their carrying capacity, evolutionary changes in traits could lead to increased population growth, and thus increased density (referred to as hard selection, Christiansen 1975). Finally, evolution in certain traits may directly affect the current extrinsic limits, that is, evolution within the population may raise or lower the carrying capacity. For instance, an evolutionary change that increases resource use efficiency would allow a greater population density to be supported at the same level of resources. It is also worth noting that there are situations in which the response to density-dependent selection may actually decrease population density. For instance, in the *B. nigra* system described previously, selection at high conspecific densities favored increased intraspecific competitive ability

at the expense of a genotype's ability to compete interspecifically. Simulations showed that this process could lead to cyclic dynamics between competing species driven by evolutionary changes in *B. nigra*'s competitive abilities (Lankau 2009). As the density of the *B. nigra* population increased, selection favored higher intra-, but lower inter-, specific competitive abilities, which allowed the other competitor species to rise in frequency. The *B. nigra* population then declined until its densities were low enough for selection to switch and favor increasing interspecific competitive ability (Lankau 2009).

Changing selection with changing density— applied considerations

We have summarized evidence that, as a species becomes more common in a community, it will be more likely to interact with other conspecifics, as well as with specialized consumers and mutualists. On the other hand, as a species becomes rarer, it will increasingly interact with heterospecific competitors, and interact as well as with generalized consumers and mutualists, as their specialists leave or die out. We have also explored the potential evolutionary consequences of these changes, as these different ecological interactions are likely to select for different trait distributions (summarized in Fig. 2). Additionally, the density of a population will affect the efficiency with which that population can respond to selection, and this evolutionary response may in turn feedback to affect density. As conservation and natural resource management largely centers on manipulating the population size of target desirable or undesirable species, we must be aware of both the ecological changes that occur as a result and the evolutionary feedbacks generated by these changes.

Many of the ecological changes described earlier lead to negative feedbacks on species abundance that could act to prevent large fluctuations in species abundance. For instance, the density-dependent build up of specialized herbivores or pathogens may prevent a species from continually increasing in density, thereby maintaining diversity in the system (Janzen 1970). These shifting selective pressures may prevent directional evolutionary changes, as selection will never be consistent long enough to produce a sustained directional response (Bell 2010). However, in human-altered systems, these feedback processes may be interrupted, either with introduced species that lack diverse selective agents from the native range that impose checks and balances, or potentially also owing to much stronger and more directional selection imposed by human activities like harvesting or pesticides. (Hendry et al. 2008). The consequences of these actions may be that species experience persistently high or low densities, densities that might be uncharacteristic of that species'

evolutionary history and that may lead to consistent selection pressures and possibly evolutionary responses. We suggest that management practices may benefit from understanding the historical density of species and the evolutionary consequences of rapid and sustained density changes.

Newly rare: persistent low density

Much conservation research and practice is geared toward protecting species that exist at perennially low densities. Knowledge about the past commonness or rarity of a species may help predict the vulnerability of current populations to extinction. For some species, this rarity is the natural condition and thus these species likely have evolved traits appropriate to low conspecific density (Kunin and Shmida 1997). However, for other species, their current rarity is a novel condition driven by anthropogenic environmental changes, and managers should be aware that these species may have trait distributions that reflect their past environment, which included higher conspecific densities. Maladaptations of newly rare taxa may include defenses geared toward specialized rather than generalized enemies, or an overreliance on specialist mutualists that cannot maintain a viable population size at their host's new, low density (Eckert et al. 2010). Additionally, animal species may have social traits that provide fitness benefits when group sizes are large (such as group vigilance or foraging) but that are ineffective or maladaptive below threshold conspecific densities (e.g., Roberts 1996). Such species may be at especially high extinction risks and would warrant special protection until their populations can rebound to historic levels or can evolve new trait values more appropriate for their new, low abundance (Honnay and Jacquemyn 2007). Again, managers must be aware that adaptation, including adaptation to rarity, may be slow and inefficient in small populations because of low genetic variation and strong genetic drift.

If low abundance threatens population persistence, then evolutionary rescue management options have sometimes been employed. Translocating individuals from other populations may be ineffective or even counterproductive, however, if those individuals are maladapted to the introduced environment. For instance, Weese et al. (2011) found that guppies from low-predation populations introduced to high-predation pools had minimal effects on population dynamics following a large disturbance because of strong selection against the migrants. While we know of no specific examples to date, it is possible that introducing individuals from a high-density population to a low-density one may introduce maladapted genes and lower average fitness. On the other hand, introducing individuals from populations with historically low

density into populations that have suffered recent population declines may introduce alleles better adapted to the new low-density biotic interactions (as well as genotypes potentially less vulnerable to inbreeding depression).

Newly common: persistent high density

Natural resource managers are often faced with problematic species that maintain persistently high densities at the expense of more desirable species. Exotic invasive species are a clear example of this, as invasive populations behind the invasion front often achieve tremendously high densities. For many invaders, this high density appears stable, although the timescale of this stability (years, decades, centuries) is still unclear for many invaders (Simberloff and Gibbons 2004). Nevertheless, management may benefit from considering the unique selection pressures acting on such species that reach unusually high densities. By escaping their complex native communities, invaders may gain not just an immediate fitness benefit from reduced consumer loads, but also evolutionary benefits by escaping the conflicting selection pressure exerted by diverse consumers. If resistance to specialists trade offs with resistance to generalists, then invaders may be free to evolve very high levels of defense against generalists without incurring the costs of increased specialist loads (Joshi and Vrieling 2005). Thus, while native species must deal with fluctuating and conflicting selection from varying ratios of generalist and specialist enemies (Berenbaum and Zangerl 2006; Zangerl et al. 2008; Bell 2010), exotic invader populations may be free to adapt to more simplified selective regimes, may be able to reduce costs of these adaptations, and may increase in both fitness and abundance.

Changing encounter rates with conspecifics and heterospecifics, with concomitant altered selection, will occur as these invasive species increase in density. When a new invasive population is first established, either at the original introduction site or along the spreading invasion front, these newly dispersed individuals will be initially rare in their new community. As a rare member of the community, these new populations may be under selection for specific traits, including being highly competitive or aggressive against other species. It is these highly competitive/aggressive individuals that will be more likely to survive and reproduce and send propagules off to continue the expansion. This may lead to the evolution of 'invasive' phenotypes that excel at invading new communities and producing new colonists before their populations build up to a high level at any one invaded site. For instance, a study comparing populations of an invasive crayfish, *Pacifastacus leniusculus*, from its native and introduced ranges found invasive populations from

streams with no native congeneric crayfish to be consistently more aggressive in their interactions with different crayfish species, as well as more voracious and active foragers and bolder in the face of predation risk (Pintor et al. 2008). As aggression, foraging rate, and boldness were correlated in these species, at high density, crayfish may be under selection to reduce their foraging rates and boldness to avoid costly aggressive interactions with conspecifics and congeners. On the other hand, invasive populations moving into crayfish-free streams may be released from this trade-off, because intraspecific interactions will be rare at least initially.

A similar process may occur in invasive plants that employ allelopathic traits to compete with heterospecifics. Allelopathy has been documented in a number of invasive plant species (Hierro and Callaway 2003) and may frequently create scenarios where the chemical traits are under different selection pressures based on the relative abundance of the allelopathic species (as described earlier for *B. nigra*). In a rapidly expanding allelopathic invader, one might predict selection for high allelochemical levels on the leading edge of the invasion, where competition is largely interspecific, but selection against the allelochemicals in well-established infestations if the invasive forms dense stands (resulting in high rates of intraspecific competition). *Alliaria petiolata* is an aggressive invader of forest understories in the eastern United States, and part of its invasive success may be because of its production of allelochemicals that negatively affect native plants and their mycorrhizal symbionts (Rodgers et al. 2008). If these allelochemicals are favored under inter-, but disfavored under intra-, specific competition, then one would expect to see the genetic investment to the chemicals decline over time in populations as they build up density. Consistent with this prediction, Lankau et al. (2009) found a strong negative correlation between the allelochemical concentration of a population and its estimated age for 44 *A. petiolata* populations dated with herbarium records, indicating a trend for higher toxicity in newly established populations.

If the low initial relative abundance of invasive species tends to select for traits that make them better competitors with native species, then managers may need to consider how their management strategies affect these selection pressures. Most invasive species management is focused on reducing the abundance of the invader, following from the logical assumption that a smaller invader population should exert less impact on native species. However, by maintaining the invader population at a lower relative abundance, this management may also maintain the selection pressures on invader traits that are harmful to native species. As a preliminary exploration of this possibility, we surveyed the land owners/managers of

the sites from which the 44 *A. petiolata* populations in Lankau et al. (2009) were collected. Of the 28 responders, 15 had performed no management of the *A. petiolata* population, and 13 had managed their invasion at some time in the past (mainly through hand pulling, with one case of herbicide spraying and one of weed whacking). For younger invasions, there was no difference in the allelochemical concentrations in managed or unmanaged populations (Fig. 3); in both cases, chemical levels were relatively high. For older invasions, chemical concentrations had dropped by about 40% in unmanaged populations. However, managed populations had maintained similarly high levels of the allelochemicals as the younger ones (Fig. 3). Thus, the pattern of declining allelochemical concentrations over time described in Lankau et al. (2009) appears to be only true for unmanaged populations. While many variables may be involved in this pattern, it is possible that by artificially maintaining the *A. petiolata* population at a lower relative abundance, management has maintained the selective value of high allelochemical concentrations. This could have consequences for native plants, as *A. petiolata* genotypes with higher allelochemical concentrations have stronger impacts on soil communities (Lankau 2010) and native plant growth (Lankau et al. 2009), and restoration of native tree seedlings is less successful in *A. petiolata* populations with high concentrations of glucosinolates (R.A. Lankau in review).

Management strategies may invoke density-dependent selection even if they have little long-term effects on

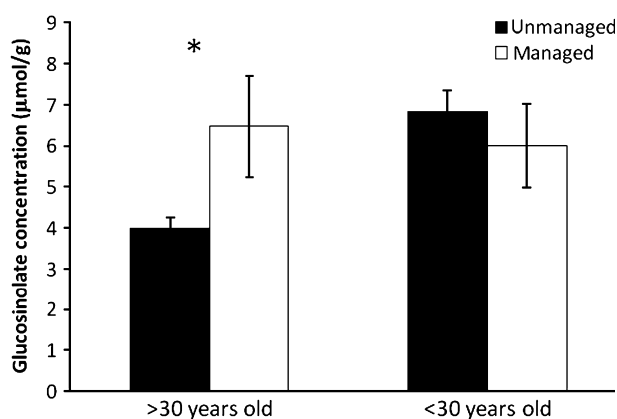


Figure 3 Mean and standard errors of root glucosinolate concentrations in *Alliaria petiolata* individuals from 28 populations grown in a common environment. Populations were divided into two age classes (estimated time since introduction to an area as determined by herbarium records) have either had no management (solid bars) or had been directly managed at some point in the past. Managed populations had significantly ($P < 0.05$) higher concentrations than unmanaged ones in the older, but not younger, age class. For more details, see Lankau et al. 2009.

population densities. For instance, in California's Central Valley, biocontrol agents released to control *C. solstitialis* (yellow starthistle) destroy 75% of seed produced, but *C. solstitialis* populations have not been strongly decreased by these agents to date (Garren and Strauss 2009). Self-thinning reduces seedling populations to the same adult densities, regardless of the presence of absence of the agent (Fig. 1). However, agents that dramatically reduce seed inputs may reduce intraspecific competition early in the life cycle and may favor traits in *C. solstitialis* that are more effective against interspecific native competitors (through reduced conspecific densities). To date, no one has examined the selective effects of biological control agents on traits of the target species as they relate to competitive ability with natives. Thus, by altering the intensity of intraspecific competition, agents may affect *qualities* of surviving plants, even if they do not affect final densities of these plants.

When will density-dependent selection matter for management?

Throughout this synthesis, we have advanced the argument that changes in the density and/or frequency of a population can have selective consequences mediated through interactions with conspecifics as well as other species. For managers and policy makers, it is important to know how frequently such selection can be expected and how strong these selection pressures will be relative to other forces acting on populations. Unfortunately, few data are available to address these questions directly. It is clear that when human activities impose direct selection on specific traits, such as body size in harvested fishes, evolutionary responses can be quite rapid (Darimont et al. 2009). It is likely the case that indirect selection imposed through changes in population density or frequency will be both weaker and less consistent, resulting in slower evolutionary responses (especially when density reductions result in loss of genetic variation and increased genetic drift). Nevertheless, many environmental changes and management practices have strong effects on density and no obvious direct selection on traits. We feel that in these scenarios, it is unwise to assume that there will be no evolutionary impact. We hope that future research will (i) determine traits under selection because of management-induced changes in density and community composition, (ii) quantify the strength of selection on these traits and compare this to direct selection imposed by management (i.e., harvesting, pesticides), and (iii) evaluate the ecological consequences of potential evolutionary responses for the focal species and its interacting community.

Conclusions

As scientists, managers, and policy makers struggle to conserve biodiversity in a rapidly changing world, they will increasingly be faced with populations with unusually high or low densities. Moreover, the primary focus of most management efforts is to cause changes in these population densities, increasing them for threatened or beneficial species and decreasing them for invasive and pest species. While numerical changes in population size may seem like a purely ecological issue, in fact these ecological changes will likely be followed by evolutionary changes, because the selective pressures on many traits will change with changing community contexts. If conservation researchers and practitioners ignore these inherent evolutionary changes, their management practices may prove less effective or even counterproductive. On the other hand, recognizing the evolutionary as well as ecological consequences of population sizes may offer new options for environmental management.

Literature cited

- Abrams, P. A. 2009 Adaptive changes in prey vulnerability shape the response of predator populations to mortality. *Journal of Theoretical Biology* **261**:294–304.
- Agrawal, A. A., J. A. Lau, and P. A. Hamback. 2006. Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology* **81**:349–376.
- Alon, M., J. Benting, B. Lueke, T. Ponge, F. Alon, and S. Morin. 2006. Multiple origins of pyrethroid resistance in sympatric biotypes of *Bemisia tabaci* (Hemiptera : Aleyrodidae). *Insect Biochemistry and Molecular Biology* **36**:71–79.
- Andow, D. A. 1991. Vegetational diversity and arthropod response. *Annual Review of Entomology* **36**:561–586.
- Antonovics, J. 1992. Towards community genetics. In R. S. Fritz, and E. L. Simms, eds. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution and Genetics*. University of Chicago Press, Chicago.
- Barry, M. J., and D. C. Logan. 1998. The use of temporary pond microcosms for aquatic toxicity testing: direct and indirect effects of endosulfan on community structure. *Aquatic Toxicology* **41**:101–124.
- Bassar, R. D., M. C. Marshall, A. Lopez-Sepulcre, E. Zandonata, S. K. Auer, J. Travis, C. M. Pringle *et al.* 2010a. Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America* **107**:3616–3621.
- Bassar, R. D., A. Lopez-Sepulcre, M. R. Walsh, M. M. Turcotte, M. Torres-Mejia, and D. N. Reznick. 2010b. Bridging the gap between ecology and evolution: integrating density regulation and life-history evolution. *Annals of the New York Academy of Sciences* **1206**:17–34 Doi: 10.1111/j.1749-6632.2010.05706.x.
- Begon, M., L. Firbank, and R. Wall. 1986. There a self-thinning rule for animal populations? *Oikos* **46**:122–124.
- Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **365**:87–97.
- Berenbaum, M. R., and A. R. Zangerl. 2006. Parsnip webworms and host plants at home and abroad: trophic complexity in a geographic mosaic. *Ecology* **87**:3070–3081.
- Bergelson, J., and C. Purrington. 1996. Surveying patterns in the cost of resistance in plants. *American Naturalist* **148**:536–558.
- Boyce, M. S. 1984. Restitution of r-selection and K-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics* **15**:427–447.
- Brichette, L., R. I. Reyer, and C. Garcia. 2001. A genetic analysis of intraspecific competition for growth in mussel cultures. *Aquaculture* **192**:155–169.
- Burdon, J. J., L. Ericson, and W. J. Muller. 1995. Temporal and spatial changes in a metapopulation of the rust pathogen *Triphragmium ulmariae* and its host, *Filipendula ulmaria*. *Journal of Ecology* **83**:979–989.
- Castillo, R. A., C. Cordero, and C. A. Dominguez. 2002. Are reward polymorphisms subject to frequency- and density-dependent selection? Evidence from a monoecious species pollinated by deceit. *Journal of Evolutionary Biology* **15**:544–552.
- Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. *Proceedings of the Ecological Society of Australia* **2**:51–78.
- Christiansen, F. B. 1975. Hard and soft selection in a subdivided population. *The American Naturalist* **109**:11–16.
- Clauss, M. J., S. Dietel, G. Schubert, and T. Mitchell-Olds. 2006. Glucosinolate and trichome defenses in a natural *Arabidopsis lyrata* population. *Journal of Chemical Ecology* **32**:2351–2373.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America* **106**:952–954.
- Davis, H. G. 2005. r-Selected traits in an invasive population. *Evolutionary Ecology* **19**:255–274.
- Duckworth, R. A., and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* **104**:15017–15022.
- Early, R., and C. D. Thomas. 2007. Multispecies conservation planning: identifying landscapes for the conservation of viable populations using local and continental species priorities. *Journal of Applied Ecology* **44**:253–262.
- Eckert, C. G., S. Kalisz, M. A. Geber, R. Sargent, E. Elle, P. O. Cheptou, C. Goodwillie *et al.* 2010. Plant mating systems in a changing world. *Trends in Ecology & Evolution* **25**:35–43.
- Einum, S., G. Robertsen, and I. A. Fleming. 2008. Adaptive landscapes and density-dependent selection in declining salmonid populations: going beyond numerical responses to human disturbance. *Evolutionary Applications* **1**:239–251.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection and evolution of mating systems. *Science* **197**:215–223.
- Ericson, L., J. J. Burdon, and W. J. Muller. 1999. Spatial and temporal dynamics of epidemics of the rust fungus *Uromyces valerianae* on populations of its host *Valeriana salina*. *Journal of Ecology* **87**:649–658.
- Eviner, V. T., and M. K. Firestone 2007. Mechanisms determining patterns of nutrient dynamics. In M. Stromberg, J. M. Corbin, and C.

- D'Antonio, eds. California Grasslands: Ecology and Management, pp. 94–106. UC Press, Berkeley, CA.
- Ewald, P. W. 1994. Evolution of Infectious Diseases. Oxford University Press, Oxford.
- Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. Annual Review of Ecology Evolution and Systematics 35:375–403.
- Ford, E. B. 1931. Mendelism and Evolution, pp. 122. Methuen and Co. Ltd., London, England.
- Ford, H. D., and E. B. Ford. 1930. Fluctuation in numbers, and its influence on variation, in *Melitaea aurinia*, Rott. (Lepidoptera). Transactions Entomology Society London 78:345–351.
- Frank, S. A. 1996. Models of parasite virulence. Quarterly Review of Biology 71:37–78.
- Fussman, G. F., M. Loreau, and P. A. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. Functional Ecology 21:465–477.
- Garren, J. M., and S. Y. Strauss. 2009. Population-level compensation by an invasive thistle thwarts biological control from seed predators. Ecological Applications 19:709–721.
- Gassmann, A. J., Y. Carriere, and B. E. Tabashnik. 2009. Fitness costs of insect resistance to *Bacillus thuringiensis*. Annual Review of Entomology 54:147–163.
- Giamoustaris, A., and R. Mithen. 1995. The effect of modifying the glucosinolate content of leaves of oilseed rape (*Brassica napus ssp. oleifera*) on its interaction with specialist and generalist pests. Annals of Applied Biology 126:347–363.
- Gratten, J., A. J. Wilson, A. F. McRae, D. Beraldi, P. M. Visscher, J. M. Pemberton, and J. Slate. 2008. A localized negative genetic correlation constrains microevolution of coat color in wild sheep. Science 319:318–320.
- Haloin, J. R., and S. Y. Strauss. 2008. Interplay between ecological communities and evolution review of feedbacks from microevolutionary to macroevolutionary scales. Year in Evolutionary Biology 2008:87–125.
- Hendry, A. P., T. J. Farrugia, and M. T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. Molecular Ecology 17:20–29.
- Hierro, J. L., and R. M. Callaway. 2003. Allelopathy and exotic plant invasion. Plant and Soil 256:29–39.
- Honnay, O., and H. Jacquemyn. 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. Conservation Biology 21:823–831.
- Horiuchi, S. 2008. High population density promotes the evolution of ownership. Ecological Research 23:551–556.
- Janzen, D. H. 1970. Herbivores and numbers of tree species in tropical forests. American Naturalist 104:501–528.
- Johnson, S. D., and K. E. Steiner. 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology & Evolution 15:140–143.
- Joshi, J., and K. Vrieling. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters 8:704–714.
- Kelly, J., and M. Scriber. 1993. Comparative detoxification of host chemicals (Magnoliaceae) by generalist and specialist saturniid caterpillars. Bulletin of the Ecological Society of America 74 (72 Suppl): 296–297.
- Kinnison, M. T., and N. G. Hairston. 2007. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. Functional Ecology 21:444–454.
- Knell, R. J. 2009. Population density and the evolution of male aggression. Journal of Zoology 278:83–90.
- Kolb, A. 2008. Habitat fragmentation reduces plant fitness by disturbing pollination and modifying response to herbivory. Biological Conservation 141:2540–2549.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant-soil feedbacks: a meta-analytical review. Ecology Letters 11:980–992.
- Kunin, W. E., and A. Shmida. 1997. Plant reproductive traits as a function of local, regional, and global abundance. Conservation Biology 11:183–192.
- Kwiatkowski, M. A., and B. K. Sullivan. 2002. Mating system structure and population density in a polygynous lizard, *Sauromalus obesus*. Behavioral Ecology 13:201–208.
- Lankau, R. A. 2007. Specialist and generalist herbivores exert opposing selection on a chemical defense. New Phytologist 175:176–184.
- Lankau, R. A. 2009. Genetic variation promotes long-term coexistence of *Brassica nigra* and its competitors. The American Naturalist 174:E40–E53.
- Lankau, R. A. 2010. Intraspecific variation in allelochemistry determines an invasive species' impact on soil microbial communities. Oecologia. Doi: 10.1007/s00442-010-1736-8
- Lankau, R. A., and S. Y. Strauss. 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. Science 317:1561–1563.
- Lankau, R. A., and S. Y. Strauss. 2008. Community complexity drives patterns of natural selection on a chemical defense of *Brassica nigra*. The American Naturalist 171:150–161.
- Lankau, R. A., V. Nuzzo, G. Spyreas, and A. S. Davis. 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. Proceedings of the National Academy of Sciences of the United States of America 106:15362–15367.
- Lankau, R. A., E. Wheeler, A. E. Bennett, and S. Y. Strauss. 2010. Plant-soil feedbacks contribute to an intransitive competitive network that promotes both genetic and species diversity. Journal of Ecology. Doi: 10.1111/j.1365-2745.2010.0173.x
- Larsson, M. 2005. Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). Oecologia 146:394–403.
- Lau, J. A. 2006. Evolutionary responses of native plants to novel community members. Evolution 60:56–63.
- Lobon-Cervia, J. 2008. Habitat quality enhances spatial variation in the self-thinning patterns of stream-resident brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 65:2006–2015.
- Loeulle, N. 2010. Consequences of adaptive foraging in diverse communities. Functional Ecology 24:18–27.
- MacArthur, R. H., and E. O. Wilson. 1967. Theory of Island Biogeography. Princeton University Press, Princeton, NJ.
- Maher, C. R., and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143:1–29.
- Mandak, B., K. V. K. Bimova, V. Mahelka, and I. Plackova. 2006a. How much genetic variation is stored in the seed bank? A study of *Atriplex tatarica* (Chenopodiaceae). Molecular Ecology 15:2653–2663.
- Mandak, B., K. Bimova., and I. Plackova. 2006b. Genetic structure of experimental populations and reproductive fitness in a heterocarpic plant *Atriplex tatarica* (Chenopodiaceae). American Journal of Botany 93:1640–1649.

- van der Meijden, E. 1996. Plant defence, an evolutionary dilemma: contrasting effects of (specialist and generalist) herbivores and natural enemies. *Entomologia Experimentalis Et Applicata* **90**: 307–310.
- Miller, T. E. 1995. Evolution of *Brassica rapa* L. (Cruciferae) populations in intra- and interspecific competition. *Evolution* **49**:1125–1133.
- Miller, T. E., and D. W. Schemske. 1990. An experimental study of competitive performance in *Brassica rapa* (Cruciferae). *American Journal of Botany* **77**:993–998.
- Mimura, M., and S. N. Aitken. 2007. Increased selfing and decreased effective pollen donor number in peripheral relative to central populations in *Picea sitchensis* (Pinaceae). *American Journal of Botany* **94**:991–998.
- Moeller, D. A., and M. A. Geber. 2005. Ecological context of the evolution of self-pollination in *Clarkia xantiana*: population size, plant communities, and reproductive assurance. *Evolution* **59**:786–799.
- Moorcroft, P. R., S. D. Albon, J. M. Pemberton, I. R. Stevenson, and T. H. Clutton-Brock. 1996. Density-dependent selection in a fluctuating ungulate population. *Proceedings of the Royal Society of London Series B - Biological Sciences* **263**:31–38.
- Morgan, M. T., W. G. Wilson, and T. M. Knight. 2005. Plant population dynamics, pollinator foraging, and the selection of self-fertilization. *American Naturalist* **166**:169–183.
- Mueller, L. D. 1997. Theoretical and empirical examination of density-dependent selection. *Annual Review of Ecology and Systematics* **28**:269–288.
- Mueller, L. D., F. Gonzalez-Candela, and V. F. Sweet. 1991. Components of density-dependent population dynamics: models and tests with *Drosophila*. *The American Naturalist* **137**:457–475.
- Nitao, J. K. 1989. Enzymatic adaptation in a specialist herbivore for feeding on Furanocoumarin-containing plants. *Ecology* **70**:629–635.
- Palkovacs, E. P., and D. M. Post. 2008. Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evolutionary Ecology Research* **10**:699–720.
- Palkovacs, E. P., and D. M. Post. 2009. Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology* **90**:300–305.
- Peck, S. L. 2001. Antibiotic and insecticide resistance modeling – is it time to start talking? *Trends in Microbiology* **9**:286–292.
- Pimentel, D. 1968. Population regulation and genetic feedback. *Science* **159**:1432–1437.
- Pintor, L. M., A. Sih, and J. L. Kerby. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos* **117**:1629–1636.
- Post, D. M., and E. P. Palkovacs. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **364**:1629–1640.
- Pruitt, J. N., and S. E. Riechert. 2009. Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. *Evolution* **63**:2966–2973.
- Pruitt, J. N., S. E. Riechert, and T. C. Jones. 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour* **76**:871–879.
- Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. *New Phytologist* **170**:445–457.
- Relyea, R. A., and N. Diecks. 2008. An unforeseen chain of events: lethal effects of pesticides on frogs at sublethal concentrations. *Ecological Applications* **18**:1728–1742.
- Reznick, D., M. J. Bryant, and F. Bashey. 2002. r- and K-Selection revisited: the role of population regulation in life-history evolution. *Ecology* **83**:1509–1520.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* **51**:1077–1086.
- Rodgers, V. L., K. A. Stinson, and A. C. Finzi. 2008. Ready or not, garlic mustard is moving in: *Alliaria petiolata* as a member of eastern North American forests. *Bioscience* **58**:426–436.
- Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95–124.
- Root, K. V., H. R. Akcakaya, and L. Ginzburg. 2003. A multispecies approach to ecological valuation and conservation. *Conservation Biology* **17**:196–206.
- Roscher, C. J., O. J. Schumacher, D. Foitzik, and E. D. Schulze. 2007. Resistance to rust fungi in *Lolium perenne* depends on within-species variation and performance of the host species in grasslands of different plant diversity. *Oecologia* **153**:173–183.
- Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. *Journal of Animal Ecology* **67**:979–986.
- Saccheri, I., and I. Hanski. 2006. Natural selection and population dynamics. *TREE* **21**:341–347.
- Sargent, R. D., and S. P. Otto. 2006. The role of local species abundance in the evolution of pollinator attraction in flowering plants. *American Naturalist* **167**:67–80.
- Seifert, E. K., J. D. Bever, and J. L. Maron. 2009. Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. *Ecology* **90**:1055–1062.
- Sharpe, D. M. T., and A. P. Hendry. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evolutionary Applications* **2**:260–275.
- Shaw, R. G., G. A. J. Platenkamp, F. H. Shaw, and R. H. Podolsky. 1995. Quantitative genetics of response to competitors in *Nemophila menziesii* – a field experiment. *Genetics* **139**:397–406.
- Siemens, D. H., and T. Mitchell-Olds. 1996. Glucosinolates and herbivory by specialists (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): consequences of concentration and induced resistance. *Environmental Entomology* **25**:1344–1353.
- Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't – population crashes of established introduced species. *Biological Invasions* **6**:161–172.
- Sinclair, A. R. E., D. Chitty, C. I. Stefan, and C. J. Krebs. 2003. Mammal population cycles: evidence for intrinsic differences during snowshoe hare cycles. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **81**:216–220.
- Sober, V., T. Teder, and M. Moora. 2009. Contrasting effects of plant population size on florivory and pollination. *Basic and Applied Ecology* **10**:737–744.
- Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* **8**:145–171.
- Stermitz, F. R., G. N. Belofsky, D. Ng, and M. C. Singer. 1989. Quinolizidine alkaloids obtained by *Pedicularis semibarbata* Scrophulariaceae from *Lupinus fulcratus* Leguminosae fail to influence the specialist herbivore *Euphydryas editha* Lepidoptera. *Journal of Chemical Ecology* **15**:2521–2530.

- Strauss, S. Y., and R. E. Irwin. 2004. Ecological and evolutionary consequences of multispecies plant–animal interactions. *Annual Review of Ecology Evolution and Systematics* **35**:435–466.
- Tabashnik, B. E. 1994. Evolution of resistance to *Bacillus thuringiensis*. *Annual Review of Entomology* **39**:47–79.
- Thrall, P. H., and J. J. Burdon. 2003. Evolution of virulence in a plant host–pathogen metapopulation. *Science* **299**:1735–1737.
- Walsh, M. R., and D. N. Reznick. 2008. Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. *PNAS* **105**:594–599.
- Weese, D. J., A. K. Schwartz, P. Bentzen, A. P. Hendry, and M. T. Kinnison. 2011. Eco-evolutionary effects on population recovery following catastrophic disturbance. *Evolutionary Applications* **4**:354–366.
- Williamson, M. S., D. MartinezTorres, C. A. Hick, and A. L. Devonshire. 1996. Identification of mutations in the housefly para-type sodium channel gene associated with knockdown resistance (kdr) to pyrethroid insecticides. *Molecular and General Genetics* **252**:51–60.
- Zangerl, A. R., M. C. Stanley, and M. R. Berenbaum. 2008. Selection for chemical trait remixing in an invasive weed after reassociation with a coevolved specialist. *Proceedings of the National Academy of Science* **105**:4547–4552.