

Rapid Evolutionary Change and the Coexistence of Species

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Abstract

Understanding the forces that allow multiple species to coexist remains a central focus of community ecology. Building evidence that evolutionary changes frequently occur on timescales relevant for ecological dynamics suggests that a complete understanding of the maintenance of diversity is likely to require incorporation of evolutionary dynamics. Coexistence mechanisms can be classified into two groups on the basis of whether they reduce inherent differences in species performance (equalizing effects) or buffer against extinction by providing advantages to rare species (stabilizing effects). Theoretical and empirical evidence suggests that rapid evolution can increase equalizing and/or stabilizing effects in several ways. Directional evolutionary changes can result in new ecological conditions that are more equal or stable than the initial state. Additionally, coevolution between competitors or consumers can lead to cyclic dynamics that provide novel evolutionary equalizing or stabilizing effects.

INTRODUCTION

Biological communities contain a bewildering diversity of life, and understanding how this diversity is maintained has long been a central goal of ecology (Chesson 2000, Hutchinson 1959, MacArthur & Levins 1967, Volterra 1926). This debate intensified with the development of neutral theory, which questioned the demographic importance of many of the biological differences studied by ecologists (Bell 2001, Hubbell 2001). However, it is now recognized that niche (species differences) and neutral (stochastic forces and dispersal limitation) processes occur in all communities to some degree (Adler et al. 2007, Chesson 2000), and progress in this area will require investigation of how these two types of processes play out in different systems.

A sometimes subtle theme running through much of coexistence research is the role of evolution in shaping communities (Dayan & Simberloff 2005, MacArthur & Levins 1967, Urban & Skelly 2006). Because all organisms are the product of past and current evolutionary forces, our understanding of species coexistence will be incomplete if we do not consider how natural selection and other evolutionary processes determine the biological properties that allow for coexistence. Will the coevolution of competitors tend to create stable, diverse communities, or will it regularly lead to the exclusion of species? The goals of this review are to explore our current understanding of that question and to organize the disparate literature on the topic into the framework of the coexistence theory established for ecological studies (Chesson 2000).

The role of evolutionary change in ecological dynamics has received increasing attention as evidence mounts that evolution can occur on a timescale commensurate with numerical population changes. In this review I consider rapid evolution to be changes in gene frequency in a population that occur on a timescale similar to that of ecological dynamics (Carroll et al. 2007, Hairston et al. 2005, Kinnison & Hairston 2007). Eco-evolutionary feedbacks can occur when the rapid evolutionary change alters ecological processes, such that understanding the ecological dynamics of a system requires considering genetic changes (Bailey et al. 2009, Fussmann et al. 2007, Kinnison & Hairston 2007, Pelletier et al. 2009). Rapid evolution has been observed in systems from microbes to vertebrates (Baquero & Blazquez 1997; Darimont et al. 2009; Dlugosch & Parker 2008; Hairston et al. 2005; Johnson & Stinchcombe 2007; Strauss et al. 2006, 2008; Whitney & Gabler 2008; Yoshida et al. 2003); notable examples include responses to anthropogenic stressors such as antibiotic, pesticide, and herbicide resistance (Baquero & Blazquez 1997, Denholm & Rowland 1992, Powles & Yu 2010, Tabashnik 1994, van den Bosch & Gilligan 2008) as well as changes in body size and life history in harvested fish (Darimont et al. 2009). Examples in relatively unimpacted systems, including fish in Trinidad (Olendorf et al. 2006, Walsh & Reznick 2008) and finches on the Galápagos Islands (Grant & Grant 2006, Hendry et al. 2009), suggest that rapid evolution may be a relatively common phenomenon. If so, then it will be vital to consider how contemporary evolution will affect our basic understanding of ecological processes. In this article I explore how the evolutionary lability of species traits can fundamentally alter our understanding of how diversity is maintained in ecological communities.

THEORETICAL FRAMEWORK FOR COMPETITIVE COEXISTENCE

In recent years the plethora of diversity-maintaining mechanisms has been organized around two general classes: mechanisms that promote diversity by creating qualitative differences between species and those that allow diversity owing to the ecological similarity of species. Both general classes can work within a given system, as exemplified by the framework developed by Peter Chesson (2000).

In this framework, the balance between equalizing and stabilizing forces determines coexistence. Equalizing forces reduce the mean fitness differences between competing species, thus

ECOLOGICAL VERSUS EVOLUTIONARY FITNESS

Fitness has been used to describe subtly different concepts in the evolutionary and ecological literature. In discussions of species coexistence, each competing species has a mean fitness measured in terms of its population growth rate (Adler et al. 2007, Chesson 2000). A species' fitness in this ecological sense is a function of its degree of adaptation to a given environment, independent of other species, which involves the species' resource availability and use, natural enemy pressure, and physical tolerances. Fitness differences between species are differences that occur independent of the relative frequency of the competing species (Adler et al. 2007, Chesson 2000). Adler et al. (2007) and Levine & HilleRisLambers (2009) provide methods for measuring fitness differences in field populations that require a combination of experimental and modeling approaches. In evolutionary discussions, fitness is typically considered at the individual organism level and measures the contribution of that individual's offspring to the next generation. I attempt to make these distinctions clear by referring to a species' ecological fitness or an individual's evolutionary fitness, while recognizing that the concepts are related. The key distinction is that a species' ecological fitness is measured relative to that of the other competing species, whereas an individual's evolutionary fitness is measured relative to that of the other conspecific individuals within its population. This distinction means that selection can potentially favor traits that increase an individual's evolutionary fitness but collectively decrease the species' ecological fitness.

making coexistence more likely. In this framework a species' mean fitness refers to the component of its population growth rate that is independent of its density and the density of competing species (see the sidebar on Ecological Versus Evolutionary Fitness for a further discussion of ecological fitness versus the traditional evolutionary understanding of the term). If two species are perfectly equal in their mean fitness, then no deterministic competitive winner exists, and the species may coexist for an extended period of time before one or the other randomly drifts to extinction. The greater the difference in mean fitness, the faster and more predictable competitive exclusion becomes. Equalizing forces include all processes that reduce the fitness differences between competitors without acting in a density-dependent fashion.

Even if species have different mean fitness values, they may still coexist if there exist sufficient stabilizing forces to overcome this difference. Stabilizing forces are those that favor the rarer species; these rare-species advantages will tend to prevent extinction because the per capita population growth rate will increase as the population size declines. To be truly stabilizing, such forces must act for all species as they become rare, such that all species in the community are buffered from declining to unsustainable population sizes. Generally, this symmetrical rare-species advantage arises through negative density (or frequency)-dependent processes, such that the per capita population growth rate is an inverse function of the population density. Density-dependent processes abound in nature on a variety of spatial scales and can include resource competition, disease, and predation or herbivory (Freckleton & Lewis 2006, Hixon et al. 2002, Rodenhouse et al. 1997, Seitz et al. 2001). Unlike equalizing forces, stabilizing forces can occur only if some degree of ecological distinction exists between species (for instance, in their resource requirements, susceptibility to enemies, or response to environmental fluctuations). Density-dependent processes occurring in ecologically distinct species will act to concentrate competition within versus between species. Thus, stabilizing forces also can be viewed as those processes that increase intraspecific relative to interspecific competition. These processes can occur through simple trade-offs between resource needs and acquisition rates (Tilman 1982) or life-history traits (competition versus colonization; Clark et al. 2004), but they can also manifest in more subtle ways as species-specific responses to environmental fluctuations (Chesson & Huntly 1997). These

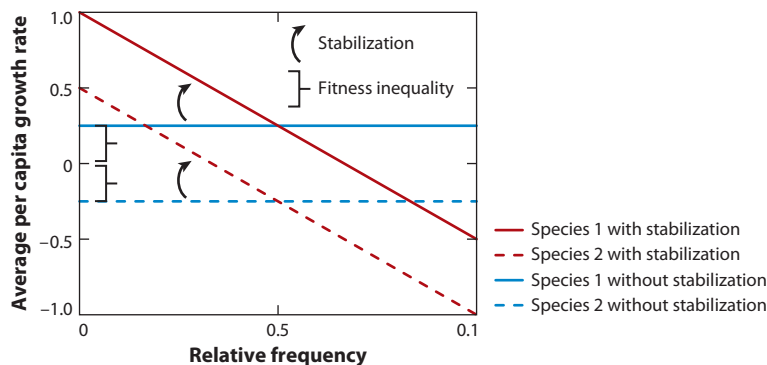


Figure 1

Stabilization is measured as a negative correlation between per capita population growth rates and a species' relative frequency (*red lines*). A species' ecological fitness is represented by the population growth rate in the absence of stabilization (*blue lines*). The solid and dashed lines refer to two different hypothetical species. Reproduced with permission from Adler et al. (2007).

species differences may occur in high dimensions, as evidenced by higher correlations among conspecific versus heterospecific individuals in their responses to environmental gradients (Clark et al. 2007).

Coexistence versus exclusion is determined by the balance of equalizing and stabilizing forces (Figure 1). Strong equalizing forces will make coexistence more likely but by themselves will not lead to long-term coexistence. Stabilizing forces can lead to long-term coexistence, but only if the ecological fitness differences between the species are not too great. In this review I use this framework to explore how contemporary evolution within species may affect the coexistence of competing species by investigating how evolutionary processes may affect both equalizing and stabilizing forces. This includes situations in which evolutionary change in one or multiple species leads to ecological conditions more conducive to competitive coexistence (by increasing stability or reducing inequality) as well as situations in which evolutionary processes lead to novel equalizing and stabilizing effects. Given the long history of research into species coexistence, I make no attempt to provide a comprehensive review. Rather, I aim to provide illustrative examples, both theoretical and empirical where possible, of the ways in which rapid evolution can affect the potential for coexistence.

EVOLUTIONARY PROCESSES PROMOTING EQUALITY

Most investigations of coexistence focus on phenomena that lead to stabilizing effects. However, because the magnitude of stabilizing effects necessary for long-term coexistence is determined by the difference in ecological fitness between competing species, we cannot ignore forces that act to make species more or less equal. Evolutionary processes that reduce the dominant species' ecological fitness, or increase the subordinate species' ecological fitness, will tend to make coexistence more likely.

Spatial Heterogeneity and Local Adaptation as Equalizing Processes

Populations separated in space often face unique environmental conditions in their local habitat, such that the optimal trait value for the local conditions differs from the species mean. Depending

upon the strength of local selection and the rate of gene flow from other sites, a population may respond to heterogeneity by local adaptation (Kawecki & Ebert 2004, Savolainen et al. 2007). Local adaptation is likely to increase a species' ecological fitness at that site (Hereford 2009, Kawecki & Ebert 2004) by, for example, maximizing resource use efficiencies, expanding environmental tolerances, or optimizing the balance of growth versus natural enemy defense (Kawecki & Ebert 2004, Savolainen et al. 2007). This adaptation will increase the likelihood of coexistence if the competitively inferior species benefits most from local adaptation but may decrease it if the reverse is true.

The potential for local adaptation in a given population is a function of (*a*) the strength of local selection, (*b*) the rate of maladaptive gene flow from other populations, (*c*) the available genetic variation within the population, and (*d*) population size, which will affect the efficiency of selection versus genetic drift (Kawecki & Ebert 2004). Importantly, the last three processes may be expected to differ predictably between common, competitively dominant species and rare, competitively inferior species. The rate of maladaptive gene flow will depend on the dispersal capabilities of the species and the number and spatial arrangement of neighboring populations. On one hand, regionally common and widespread species often have fairly connected populations; this may lead to high rates of gene flow, which tend to inhibit local adaptation. For instance, populations of a cricket species from across its continuous distribution in continental Europe showed no evidence of latitudinal clines, whereas those from latitudinally matched but isolated populations from islands and peninsulas did display a pattern of local climate adaptation (Cassel-Lundhagen et al. 2011). Thus, ecological fitness differences may be decreased if high rates of maladaptive gene flow slow local adaptation in very common species. On the other hand, regionally rare species are more likely to be genetically isolated from conspecific populations, a circumstance that could make local adaptation more likely. However, small, fragmented populations often suffer from low genetic variation, as alleles are lost to drift, and may exhibit inefficient responses to selection because stochastic forces play a larger role in their evolution (Amos & Balmford 2001, Kinnison & Hairston 2007, Ouborg et al. 2006). If a competitively inferior species has too little genetic variation or too small of a population size to respond efficiently to local selection pressures, the ecological fitnesses of common and rare species will diverge, and competitive exclusion is a likely outcome.

Genetic Correlations and Trade-Offs as Equalizing Forces

A species' ecological fitness may change owing to evolutionary changes in traits seemingly unrelated to competition if those traits show a genetic correlation with competitive ability (Lande & Arnold 1983). This correlation may occur for traits involving increased defense or stress tolerance, which can impose costs. For instance, *Drosophila* populations subjected to many generations of selection by parasitoids show reduced larval competitive ability (Kraaijeveld et al. 2001). Costs of defensive traits have been found in several systems (Koricheva 2002); similarly, selection for increased tolerance to particular stresses, such as desiccation or toxic heavy metals, can trade off with competitive ability and thus affect the equality between competitors. Stress tolerance and competitive ability often trade off between species (Grime 1977) and can also exhibit trade-offs among genotypes intraspecifically (He et al. 2010, Stanton et al. 2004). Whether individual-level costs translate into population-level effects is not clear but is a necessary condition for costs to influence coexistence. As with local adaptation, the consequence of these evolutionary changes for coexistence depends on whether the dominant or subordinate species experiences the costs. For instance, common, dominant species may support higher consumer loads and thus experience greater selection for resistance. Equality in ecological fitness would increase if the population evolves to a new optimum resistance level that results in decreased competitive

ability. If the direction of selection cycles with host abundance, it can provide additional stability (see below).

Niche Convergence as an Equalizing Process

Finally, equality can evolve if selection drives species to become more similar in their niches, which is in contrast to the well-studied process of species divergence via character displacement (see below). In diverse communities, species may be selected to converge on the most abundant niche under certain conditions. Hubbell (2006) simulated evolution of niche preferences in a suite of species with restricted dispersal in a spatially heterogeneous environment. When the environment was spatially autocorrelated and patchy and species' initial positions were clumped, species diverged by specializing on the particular region of the niche spectrum in which they were placed initially. Such a process would potentially reduce equality (if the different niche regions provided for differing ecological fitness) but increase stability (see below). However, dispersal limitation coupled with a fine-grained environment led to convergent evolution, with all species evolving to specialize on the most common niche. This occurred because high species diversity and limited dispersal created a situation in which interactions between any two species were relatively rare. Thus, the selection imposed by any one species on another was never consistent enough to cause pair-wise coevolutionary patterns. An alternative pattern was observed when the environment was coarsely scaled but the initial location of individuals was randomized, such that each species experienced a wide range of environments. In this case, species evolved to become polymorphic generalists. In these latter two cases, the evolutionary convergence of species would tend to reduce any differences in ecological fitness between them. Thus, competitive exclusion would be extremely slow, and in fact extinctions were not observed in these simulations run over 1,000 generations (Hubbell 2006). However, this evolution of species equivalence would also likely act to reduce stabilizing effects, so that if a species were to drift to low abundance, no deterministic force would act to increase the species' population growth rate and prevent extinction.

EVOLUTIONARY PROCESSES PROMOTING STABILITY

Evolutionary processes that increase negative density dependency or strengthen intraspecific relative to interspecific competition will tend to promote stability, because these changes will favor the rarer species. Three stability-promoting processes are described in detail below: (a) genetic variation in trait values per se, even without changes in the mean trait value of a population; (b) directional change in a population's mean trait value, such that coexistence is more stable at the new evolutionary equilibrium; and (c) cyclic changes in mean trait values in which selection pressures shift direction through time and prevent the population from achieving a fixed optimal trait value.

Standing Genetic Variation in Competitive Ability Can Promote Coexistence

Even in the absence of evolutionary changes in trait values, genetic variation within a population may promote stability. Heterogeneity within a population can stabilize coexistence if the phenotypic classes that respond most strongly to spatial or temporal environmental gradients are also the ones that competition affects most [the storage effect of Chesson & Huntly (1997)]. Storage effects, or more generally subadditive dynamics, are often studied with respect to life-history stages (seeds versus seedlings, larvae versus adults) but could also arise owing to distinct genotypes (Chesson 1990). Genetic variation in environmental response could be combined with

spatial genetic structure such that some genotypes respond more strongly to good environments, but this also causes the genotypes to compete more strongly owing to the response of related neighbors. Alternatively, populations might harbor a genetic trade-off between environmental response and competitive ability, such that genotypes that respond most strongly to favorable environments are also the least effective and/or most sensitive competitors. For instance, Donohue and colleagues (Donohue et al. 2005a,b) found that different genotypes of the model plant *Arabidopsis thaliana* showed divergent germination responses in different locations, and the germination phenotype had strong impacts on lifetime fitness. If these populations were spatially genetically structured (a common occurrence in plant species with restricted distributions; Cheplick 1993, Donohue 2003), then genotypes that can take advantage of favorable environments through increased germination would be simultaneously constrained by the intense competition from the high density of their related, cogerminating neighbors. This constraint will tend to reduce the population growth of common species relative to rare ones if the rare species prefers different environmental conditions.

Genetic variation can also promote coexistence if genotypes differ in their competitive ability against other species. If all competing species contain such variation, then intransitive dynamics may occur among genotypes, even if the species form a linear hierarchy based on their mean competitive abilities (Aarssen 1989, Taylor & Aarssen 1990). Intransitive dynamics tend to disfavor whichever species is currently most common; because every type can be outcompeted by at least one other, one type becoming common sets the stage for rapid population growth of the type that can outcompete it (Laird and Schamp 2006). Although plant communities typically show transitive hierarchies at the species level (Keddy & Shipley 1989, Keddy et al. 2000), intransitive dynamics can develop between specific genotypes of competing species (Lankau & Strauss 2007, Taylor & Aarssen 1990). Therefore, even a species that is on average the worst competitor may have some genotypes that outcompete some genotypes of a different species, potentially providing a buffer against extinction.

In one of the most direct tests of whether genetic variation within species can help maintain species diversity, Booth & Grime (2003) found that artificial plant communities created with multiple genotypes per species retained more species diversity after 5 years than those that began with only one genotype per species. A subsequent study found that genotypes of a given species varied widely in their final abundance; even the most dominant species (on average) consisted of a mix of competitively superior and competitively subordinate genotypes (Whitlock et al. 2007). For most of the six species studied, a genotype's rank abundance was consistent across levels of genetic diversity in the community, which suggests that genotypes have deterministic competitive abilities (Whitlock et al. 2007). However, for some species, genotype abundance patterns were not correlated across treatments, a result that could imply genotype-genotype interactions, as suggested by Aarssen (1989). Indeed, a separate study with three genotypes of two of the dominant species from Booth & Grime's (2003) experiment found substantial evidence for genotype-genotype interactions; no one genotype of either species was competitively superior to all others (Fridley et al. 2007). Importantly for the maintenance of species diversity in a community, Fridley et al. also found that the performance of a competitively inferior species varied significantly owing to the genotype of the dominant competitor, suggesting that genetic variation within dominant species may provide competitive refuges for rare, competitively inferior species.

Directional Changes in Trait Values Can Promote Stability

If a population is genetically variable in traits related to competition, and competition is an important determinant of fitness, then trait values should change over time owing to natural selection. The idea that evolutionary change in species' niches can allow coexistence has a long history

in ecology via the study of character displacement. Character displacement occurs when two species evolve reduced niche overlap via changes in particular traits related to resource competition (MacArthur & Levins 1967). When the degree of niche overlap between species determines the strength of interspecific competition, selection can favor genotypes that are the most distinct from the competing species along a given niche axis. Through differentiation in the genotypes' resource base, interspecific competition is weakened. Consequently, intraspecific competition may be strengthened if the total resource base is relatively unchanged but the niche breadth of each species has narrowed. Ultimately, this process will increase stability by concentrating competition within rather than between species.

Evidence for character displacement has been documented in dozens of systems, including vertebrates, invertebrates, and plants (for a review see Dayan & Simberloff 2005). The majority of this evidence comes from comparisons between sympatric and allopatric populations of competing species: character displacement is inferred if the two species are more similar in their niche position (or in traits associated with competition) in allopatric as compared with sympatric populations. Such studies often give little information on the time course of these evolutionary changes; thus, it is not clear if this evolution can be considered rapid according to the definition provided above. However, for character displacement to be an important force in maintaining diversity, it generally must act on a timescale similar to or shorter than the rate of competitive exclusion. Evidence from anthropomorphically introduced species suggests that morphological changes can occur relatively rapidly (tens to hundreds of years); for example, the small Indian mongoose (*Herpestes javanicus*) has evolved increased canine size within 100–200 generations of its introduction to islands that lack its larger congeneric competitor (Simberloff et al. 2000). Additionally, population mean beak sizes of Galápagos finches can change in matter of years (Grant & Grant 2006, Hendry et al. 2009); direct observations of character displacement in beak size have been made in one finch population only 22 years after the introduction of a competitor species (Grant & Grant 2006).

Although studies of character displacement have typically focused on traits directly related to resource acquisition, directional changes in other traits may promote stability in similar ways. A series of studies by Turkington and colleagues showed that genotypes of the legume *Trifolium repens* displayed evidence of adaptation to the species with which they co-occurred (Turkington 1989, Turkington & Harper 1979) and displayed greater competitive ability against genotypes of *Lolium perenne* collected from the same versus different populations (Aarssen & Turkington 1985). Further investigation revealed that this pattern was likely due to interactions with a third party: the nitrogen-fixing symbionts of *T. repens* (Chanway et al. 1989, Thompson et al. 1990). Given the increasingly recognized importance of microbial mutualists for competition among plants (Bever 2003, Kardol et al. 2007, Klironomos 2002, Kulmatiski et al. 2008), similar dynamics may occur frequently as plant competitors interact with common mycorrhizal fungi, pathogens, or nitrogen-fixing bacteria.

Although character displacement tends to increase stability, it does not always necessarily follow that the process will increase the likelihood of coexistence because decreases in equality may offset increases in stability. When interspecific competition drives shifts in resource use, the two species may not equally divide the resource base. If one species ends up specializing on an inferior resource, this will decrease that species' ecological fitness, even if the evolutionary fitness of these specialized genotypes is higher than that of genotypes that remain adapted to the prior resource base (Rice & Pfennig 2008). For instance, Mexican and Plains spadefoot toads (*Spea multiplicata* and *Spea bombifrons*, respectively) occur in both allopatric and sympatric populations. In allopatry, both produce larvae that exist in two forms (omnivorous and carnivorous) in approximately equal proportions. However, in sympatry *S. multiplicata* produces almost entirely omnivorous larvae, whereas *S. bombifrons* produces almost entirely carnivorous larvae. Because both species grow best

on a carnivorous diet (Pfennig & Murphy 2000), *S. multiplicata* has likely experienced a net decline in ecological fitness owing to the spread of *S. bombifrons* (Rice & Pfennig 2008). If the reduction in ecological fitness for the losing species is large enough, the increased stability produced by the evolutionary change may not be sufficient to allow coexistence.

Character displacement is the predicted response when two species compete for substitutable resources, for instance, when two predator species compete for prey but can utilize several different prey species or become omnivorous to meet their nutritional needs. Many species, however, compete for essential resources for which no adequate alternative exists. In this case, character divergence is not an evolutionary option, and models predict that the two species will converge in their resource uptake phenotypes (Fox & Vasseur 2008). Somewhat counterintuitively, character convergence for essential resources can be stabilizing just like character divergence for substitutable resources. When a species must acquire two essential resources to grow (for instance, nitrogen and phosphorus in plants), selection will tend to drive trait values that lead to colimitation by the two resources (Abrams 1987). When two species compete for the same two essential resources but require them in different proportions, coevolution will drive them to evolve more similar uptake ratios in sympatry than they would in allopatry (Fox & Vasseur 2008). Consider two species that each require the same two resources but differ in which resource each requires at a higher rate. In allopatry, each species evolves a biased resource uptake that reflects the species' relative stoichiometric needs, to maintain colimitation. In other words, the species evolve to acquire as much of the most limiting resource as possible and then adjust their uptake of the less limiting resource down to the point that they are equally limited by both resources (the results are unchanged if instead the model assumes organisms acquire resources on the basis of availability and then excrete unused resources to maintain stoichiometric balance). If these species were to come into secondary contact, each would drive down the level of its primary resource to a level that would exclude the other species (because the primary resource for one species is the secondary resource of the other), and the competitive winner is determined by a priority effect (Fox & Vasseur 2008). However, coevolution between the two species in sympatry alters resource availabilities such that both species evolve less biased uptake ratios, which results in phenotypic convergence. This convergence occurs because each population is again selected to maintain colimitation by both resources, but the presence of the other species alters the resource dynamics such that colimitation requires a greater investment in acquisition of the secondary resource to achieve stoichiometric balance in sympatry (where it is less available owing to use by the other species) versus allopatry (Fox & Vasseur 2008). This process leads to a stabilizing rare species advantage because the common species will evolve essentially as if it is alone, whereas the rarer species will evolve in response to the common species and be under selection to invest more equally in acquisition of the two resources (Fox & Vasseur 2008). The outcomes of this model result from explicitly modeling the dynamics of the two resources, something that is often not considered in theories predicting character displacement.

Cyclic Evolutionary Changes Can Promote Stability

During the process of character displacement, coexistence is promoted by the directional evolution of each species toward its new optimum, at which point selection becomes stabilizing and trait values become fixed. However, species coexistence can also be promoted by evolutionary cycles, in which the direction of selection (and subsequent trait changes) constantly shifts back and forth.

Cyclic evolution may occur when the traits promoting high interspecific competitive ability are negatively genetically correlated with those promoting high intraspecific competitive ability (Lankau 2009, Leon 1974, Levin 1971, Pease 1984, Pimental et al. 1965). On one hand,

selection is expected to favor increased intraspecific competitive ability when a population is common, because most interactions will be conspecific, but to favor interspecific competitive ability when the population is rare and interacts mostly with heterospecifics (Pimental et al. 1965). If these traits are negatively correlated, then selection for increased intraspecific competitive ability in the common species will tend to reduce that species' interspecific competitive ability, thus favoring the competitively inferior species (Pease 1984). On the other hand, when a species is rare, selection for increased interspecific competitive ability will provide a demographic benefit, and the correlated decrease in intraspecific ability will have little negative consequence. Because the selective pressures on competitive traits are determined by the relative abundance of conspecifics versus heterospecifics, as an initially rare species increases in abundance, selection pressures may eventually switch, leading to cyclic dynamics. Taken together, this process will always tend to favor the rarer species and thus to promote the stability of coexistence (Lankau 2009, Pease 1984).

Coexistence via genetic trade-offs in competition has been studied theoretically and empirically for decades. In laboratory experiments on competing houseflies and blowflies, Pimental et al. (1965) found that houseflies were initially dominant, but after approximately 25 generations blowflies increased rapidly in abundance with a subsequent decline in housefly numbers. Similar patterns were observed in competition between different *Drosophila* species under certain environmental conditions (Ayala 1966). Although the exact role of genetic changes relative to changing environmental conditions is difficult to separate in these experiments (Arthur 1982, Ayala 1969), theoretical investigations into this "reversal of dominance" have repeatedly shown the potential for this process to promote coexistence (Leon 1974, Levin 1971, Pease 1984). Whether approached graphically (Leon 1974), numerically (Levin 1971), or analytically (Pease 1984), and regardless of whether the trait was modeled with single-locus haploid or quantitative inheritance, a negative genetic correlation between intra- and interspecific competitive ability proved necessary for competitive dynamics to shift. In an analytical model, Pease (1984) found simple conditions for coexistence versus exclusions that mirrored those in the familiar Lotka-Volterra competition models. However, in this case the outcome of competition was determined by the genetic variance and covariance of the competition coefficients rather than their magnitude.

Evidence for negative genetic correlations between intra- and interspecific competitive ability has been found in many cases, including the dipteran examples described above as well as a handful of plant and vertebrate systems (Duckworth & Badyaev 2007, Lankau & Strauss 2007, Shaw et al. 1995). Genetic correlations between behavioral traits, sometimes referred to as behavioral syndromes or animal personalities, may lead to these negative correlations. For instance, western bluebirds were extirpated from large areas of their range owing to logging and agriculture but are now reestablishing populations in those areas owing to the increase in artificial nest boxes (Duckworth & Badyaev 2007). In doing so, they are largely excluding mountain bluebirds, which had remained in the area. By comparing western bluebird populations on the leading edge of the range expansion with older populations, Duckworth & Badyaev (2007) found that the colonizers, which compete largely with their congeners for nest sites, tended to be more aggressive than individuals from older populations that compete mostly intraspecifically. This difference may be due to a negative correlation between male aggressiveness and parental behavior (Duckworth 2006). Experimental manipulation of densities showed that aggressive males were better at dispersing to newly opened habitat and had higher fitness there, but they had lower fitness than nonaggressive males in established populations (Duckworth 2008). Although the long-term outcome of this interaction is unclear, it may eventually allow the reestablishment of mountain bluebird populations, although the inherent advantages of western bluebirds (i.e., lack of equality) in these environments may outweigh any evolutionary increase in stability.

Plants are often assumed to compete for the same basic resources in more or less the same ways. Such simplicity of resource competition would likely drive positive correlations between intra- and interspecific competitive ability; e.g., in a nitrogen-limited system, a genotype with improved nitrogen acquisition traits would be a stronger competitor against both conspecifics and heterospecifics. However, negative genetic correlations have been observed in at least three plant species. *Nemophila menziesii* genotypes with the highest fitness when grown in monocultures tended to have the lowest fitness when grown with an interspecific grass competitor, although the mechanisms behind this trade-off are unclear (Shaw et al. 1995). Interestingly, this pattern was not observed in a greenhouse study with these same species, which suggests that the trade-off may be expressed only in complex field environments (Shaw & Platenkamp 1993). In a series of studies investigating competition between *Brassica nigra* and three unrelated species, *B. nigra* genotypes artificially selected to produce high concentrations of a secondary compound (sinigrin) consistently performed well when competing with the heterospecifics but poorly when competing with conspecifics (Lankau 2008; Lankau & Strauss 2007, 2008). A similar process may be at play in a related species, *Alliaria petiolata*, which has been actively invading North American forest understories since its introduction from Europe approximately 150 years ago (Rodgers et al. 2008). As with *B. nigra*, *A. petiolata* genotypes that produce high levels of sinigrin have the most negative impacts on seedlings of several native tree species (Lankau et al. 2009), and preliminary evidence suggests that this high allelochemical production reduces intraspecific competitive ability (R.A. Lankau, unpublished data). Because *A. petiolata* can displace native understory vegetation and form dense, almost monospecific stands (Rodgers et al. 2008), the balance of competition tends to shift from largely interspecific in recently colonized areas to largely intraspecific in older, established stands. Thus, one might hypothesize that investment in sinigrin would be favored along the leading edge of the invasion but disfavored in older populations. Consistent with this prediction, a comparison between *A. petiolata* genotypes from 44 populations grown in a common environment found a marked decline in sinigrin concentrations with estimated population age (Lankau et al. 2009). Additionally, vegetation surveys in Illinois found that *A. petiolata* abundance over a five-year interval tended to decline with population age, whereas the abundance of native woody species increased across this temporal gradient.

In both *B. nigra* and *A. petiolata*, the observed negative correlation seems to arise because the competitors in these systems, although they still largely require the same basic, nonsubstitutable resources, compete for those resources in different ways. Sinigrin, a glucosinolate compound characteristic of many species in the mustard family, has shown toxicity to a broad range of organisms, including insects, microbes, and other plants (Kliebenstein 2004, Raybould & Moyes 2001). In both *B. nigra* and *A. petiolata*, one important action of this compound is to reduce the abundance and diversity of arbuscular mycorrhizal fungi in soils underneath genotypes that produce high levels of the compound (Lankau 2011, Lankau et al. 2011). Like all members of the Brassicaceae family, both species are characteristically nonmycorrhizal, whereas most of their competitors benefit from the fungal association to varying degrees; therefore, a trait that reduces mycorrhizal abundance will tend to increase interspecific competitive ability. Because their conspecific neighbors are nonmycorrhizal, such a trait will not increase intraspecific competitive ability, and if the compound is costly to produce, it may reduce it. The field patterns observed between *B. nigra* and its heterospecific competitors could be largely replicated in the greenhouse by growing plants in soils collected under patches of high- or low-sinigrin *B. nigra*, or other species. However, these patterns disappeared when arbuscular mycorrhizal fungi were filtered out of the soils (Lankau et al. 2011). In this case, the negative trade-off between intra- and interspecific competition was driven by the different competitive mechanisms used by *B. nigra* to compete with heterospecifics (indirect allelopathy, a form of interference competition) versus conspecifics (scramble

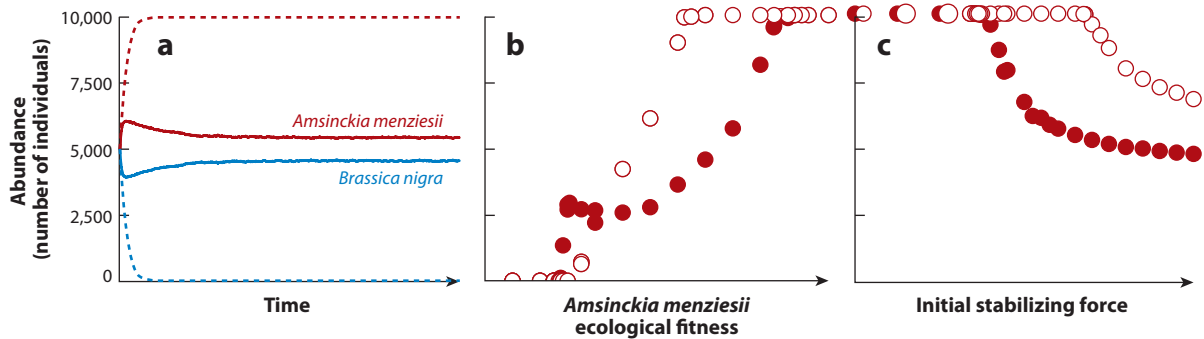


Figure 2

Results of simulated competition between *Brassica nigra* and *Amsinckia menziesii*, parameterized with data from Lankau & Strauss (2007). (a) Average abundances from 10 replicate runs. Red lines, *A. menziesii*; blue lines, *B. nigra*. Solid lines, simulations with genetic variation in *B. nigra*; dashed lines, simulations with no genetic variation. (b) Final abundance of *A. menziesii* after 1,000 generations in simulations varying in the initial ecological fitness of *A. menziesii*. Solid circles, simulations with genetic variation and evolution; open circles, simulations with no genetic variation. (c) Final abundance of *A. menziesii* after 1,000 generations in simulations varying in the initial magnitude of the stabilizing force. Symbols as in panel b. Adapted with permission from Lankau (2009).

competition). When different competitive mechanisms (such as interference, scramble, or pre-emption) are used for inter- versus intraspecific competition, the stability-promoting negative correlation can arise even if all competitors compete for the same basic resources.

Whether or not a genetic trade-off between competitive abilities as described will actually result in coexistence via evolutionary change will depend on both the mode and tempo of evolution and the inherent ecological relationships between the competing species. Using the observed data on genetic variation and covariation in competitive abilities in *B. nigra* and the stability and equality of competition between the mean *B. nigra* genotype and its three heterospecific competitors, individual-based simulations found that in the absence of evolutionary change, long-term coexistence was possible only for one of the three species pairs (Lankau 2009). However, when *B. nigra* was allowed to evolve according to the observed data, all three species pairs coexisted in the long term (Lankau 2009). Additionally, the observed levels of genetic variation allowed for coexistence across a much wider range of ecological scenarios than the nonevolutionary simulations, including scenarios in which the competing species were both less equal in mean fitness and less ecologically stable (i.e., their starting parameter values did not provide sufficient stability for coexistence; **Figure 2**). Because this simulation study was tailored to a particular system, the generality of these results is unknown. A different simulation study dealing with a similar framework found that stability depended on the mating system (sexual versus asexual) and spatial structure (well-mixed versus spatially clustered); sexual reproduction and spatial structure tended to destabilize the system (Vellend & Litrico 2008). In this framework, selection tends to favor extreme phenotypes (depending on the relative abundance of the species), but sexual reproduction continually produces intermediate phenotypes, slowing the rate of phenotypic change and allowing ecological dynamics to fluctuate more wildly before evolutionary changes can modulate them. In asexual systems, localized dispersal and competition tended to increase stability, as has been found in other intransitive systems (Kerr et al. 2002). However, with sexual reproduction, simulations with local dynamics were less stable than those with no spatial structure. The creation of distinct monospecific patches led to an increase in intraspecific relative to interspecific interactions such that relatively few areas imposed selection for increased interspecific competitive ability. Owing to constant gene flow from central to edge individuals from sexual reproduction, the

genetically variable species tended to be excluded by the nonevolving competitor (Vellend & Litrico 2008).

In addition to the direct coevolution between competitors discussed above, evolutionary cycles driven by coevolution with other trophic levels can promote competitive stability if the traits under selection are genetically correlated with traits important for competitive ability. Natural enemies (such as predators, diseases, or herbivores) can provide a purely ecological stabilizing force if they act in a density-dependent fashion, imposing greater per capita effects on the more common species (Burdon et al. 1995, Chesson 2000, Ericson et al. 1999, Root 1973). However, there is considerable evidence that interactions with consumers can drive rapid evolution of resistance and/or tolerance in host species (Kraaijeveld et al. 2001, Meyer et al. 2006, Zangerl & Berenbaum 2005). If resistance or tolerance trades off with competitive ability, then selection for increased resistance in one species could allow an inferior competitor to coexist. For instance, evolutionary increases in resistance to both microparasites and parasitoids in *Drosophila melanogaster* led to correlated reductions in larval competitive ability (Kraaijeveld et al. 2001, Vijendravarma et al. 2009). Alternatively, a release from consumer pressure could allow a species to evolve reduced investment in resistance/tolerance and subsequently greater competitive ability, a phenomenon studied intensively in exotic introductions with mixed results (Joshi & Vrieling 2005, Muller & Martens 2005, Siemann & Rogers 2001, van Kleunen & Schmid 2003, Willis et al. 2000). If the consumed species simply evolves to a new optimum trait value and then remains steady, this will mostly affect the equality of the system (increasing or decreasing equality, depending on the prior competitive hierarchy). However, if consumer populations track host density, this could lead to cyclic evolutionary responses that provide additional stability. In this case, the common host species would be under selection to reduce its competitive ability to increase resistance. However, rarer species would face reduced consumer pressure and so would be free to reduce resistance to increase competitive ability. As the species' relative abundance increases owing to its improved competitive ability, it will build up higher consumer loads, and eventually selection for resistance traits will increase. Such a cycle would tend to provide an additional evolutionary advantage to whichever species is rarer, thus increasing stabilizing forces and competitive stability.

Although empirical support exists for all of the steps in this process [i.e., density-dependent consumption (Burdon et al. 1995, Root 1973), evolutionary responses of hosts to consumers (Meyer et al. 2006, Zangerl & Berenbaum 2005), and negative genetic correlations between resistance/tolerance and competitive ability (Kraaijeveld et al. 2001, Yoshida et al. 2004)], I am not aware of any systems in which this entire process has been documented. However, chemostat studies of predator-prey dynamics with rotifers and algae showcase the power of natural enemies to shape resistance evolution in their prey and the consequences of this evolution for ecological dynamics (Yoshida et al. 2003). In this case, the algal species faced a trade-off between resistance to predation and competitive ability that was determined by cell size. As the rotifer population increased, it selected for more resistant algae. This increase in resistance then led to a decline in the rotifer population, relaxing selection on resistance and allowing the more competitive, smaller-sized algal genotypes to dominate. In turn, these more susceptible algae allowed the rotifer population to rebound, and the cycle started again. Although this experiment dealt only with a single algal species, it seems plausible that the evolutionary cycles driven by fluctuating rotifer populations could have important consequences for competitive outcomes in multispecies algal communities.

SYNTHESIS

Understanding how multiple species can coexist in a community despite intense competition remains one of the central goals of ecology. In addition to its theoretical interest, such an

Table 1 Example mechanisms of species coexistence via rapid evolution

Ecological coexistence forces increased by rapid evolution	
Equalizing forces	Local adaptation
	Correlated selection for resistance/tolerance to biotic or abiotic stress
Stabilizing forces	Character displacement (niche divergence)
	Character convergence (essential resources)
Novel evolutionary coexistence forces provided by rapid evolution	
Equalizing force	Niche convergence
Stabilizing forces	Genetic trade-offs in intraspecific- versus interspecific competitive ability
	Coevolution with natural enemies

understanding is vital to combating applied issues such as species extinctions and invasions. Although the mechanisms maintaining diversity encompass a rich set of biological processes, they can be organized profitably within the framework of equalizing and stabilizing effects put forth by Chesson (2000). Ultimately, both a species' ecological fitness and its degree of negative density dependency will depend on its traits and how they interact with the abiotic and biotic environments. Because the traits of organisms are shaped by past and current evolutionary forces and building evidence suggests that a clear distinction generally does not exist between ecological and evolutionary time, a full understanding of competitive coexistence must incorporate the potential for evolutionary changes in species' traits during the competitive interaction.

Clearly, contemporary evolution has the potential to affect coexistence via both equalizing and stabilizing effects. These evolutionary coexistence mechanisms can themselves be categorized into two broad categories: those that increase traditional ecological equalizing/stabilizing effects and those that provide novel evolutionary equalizing/stabilizing effects (**Table 1**). Evolutionary processes can strengthen ecological coexistence mechanisms by leading to new trait values that either reduce species fitness differences or increase intraspecific relative to interspecific competition (**Figure 3a**). For instance, local adaptation in the subordinate species tends to increase its ecological fitness and thus reduce the system's inequality. Similarly, character displacement in two competing species results in species that specialize on different resources, thus increasing the strength of intraspecific competition and weakening the strength of interspecific competition. In both cases, evolutionary optimization leads to a new ecological state that is more equal/stable than the starting point, at which point evolutionary changes slow or stop. Alternatively, novel evolutionary mechanisms occur when adaptive landscapes are structured or shift in such a way that selection consistently drives the convergence of species or provides an evolutionary advantage to the rare species (**Figure 3b**). For instance, diffuse interactions with diverse competitors combined with restricted dispersal in fine-grained environments consistently lead to species convergence on the most common niche, and will continue to do so if the frequency of niches fluctuates through time. Similarly, genetic trade-offs between inter- and intraspecific competitive ability provide rare species with an evolutionary advantage because they will be selected to maximize competitive ability against the common species, whereas the common species is selected to maximize competitive ability against itself. These processes differ from the earlier examples because they do not depend on reaching a particular new ecological condition but rather provide an overarching evolutionary force that results in constantly shifting ecological conditions (**Figure 3**).

As biodiversity declines at both the species (Pimm & Raven 2000, Wilson et al. 2007) and genetic levels (Geburek & Konrad 2008, Ledig 1992, Ouborg et al. 2006), understanding the mechanisms that promote diversity becomes increasingly important. Given the increasing calls

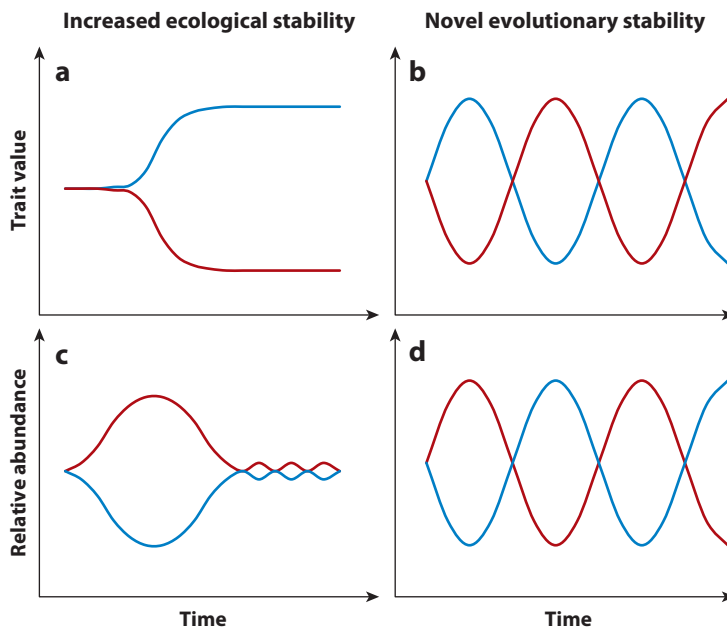


Figure 3

Example genetic (*a,b*) and numerical (*c,d*) dynamics of a system in which rapid evolution leads to increased ecological stabilizing effects (*a,c*; for example, owing to character displacement) and a system in which rapid evolution provides a novel evolutionary stability (*b,d*; for example, owing to trade-offs between intra- and interspecific competitive ability). The red and blue lines indicate the two hypothetical competing species.

for a unification of evolutionary and community ecology (Haloïn & Strauss 2008, Hughes et al. 2008, Johnson & Stinchcombe 2007) and the central role of biodiversity maintenance in the development of community ecology as a scientific discipline (Chesson 2000, MacArthur & Levins 1967, Tilman 1982), further research into the role of evolution in the coexistence of species seems warranted. It is my hope that situating future research within the framework of stabilizing and equalizing effects will help direct these future efforts. Additionally, future research would benefit from recognizing situations in which evolutionary change increases the ecological mechanisms of coexistence and those in which evolutionary processes provide novel stabilizing or equalizing forces that could not be predicted from ecological interactions alone.

FUTURE ISSUES

1. Additional research should investigate the phenotypic and genetic differences between coexisting and geographically distinct populations of competing species, with an emphasis on the outcome of competitive interactions in addition to observable trait differences, to determine whether coevolution tends to reduce or exacerbate competitive interactions.
2. Future research would benefit from direct tests of the importance of frequency dependency for population regulation among competing species (to evaluate the role of stabilizing versus equalizing effects). An additional step would be to perform these experiments with genetically variable versus clonal populations, over multiple generations, to test whether rapid evolutionary change results in increased stability and/or equality.

3. Research in tractable systems with rapid reproduction (for instance, microbes or plankton) will be necessary to experimentally determine whether evolutionary cycles due to shifting selection from interspecific versus intraspecific competition, or rising and falling consumer loads, can lead to long-term coexistence of competitors.
4. Finally, investigations across large spatial and temporal scales using space-for-time substitutions across chronosequences, or revival of dormant propagules from datable sediment strata, could be used to test for the importance of evolutionary cycles versus directional changes for coexistence in less tractable, longer-lived species. The introduction of exotic species by humans, or range shifts due to climate change, may offer opportunities to observe the evolutionary consequences of novel competitive interactions in real time.

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