How Do Species Interactions Affect Evolutionary Dynamics Across Whole Communities?

Timothy G. Barraclough

Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, United Kingdom; email: t.barraclough@imperial.ac.uk

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Abstract

Theories of how species evolve in changing environments mostly consider single species in isolation or pairs of interacting species. Yet all organisms live in diverse communities containing many hundreds of species. This review discusses how species interactions influence the evolution of constituent species across whole communities. When species interactions are weak or inconsistent, evolutionary dynamics should be predictable by factors identified by single-species theory. Stronger species interactions, however, can alter evolutionary outcomes and either dampen or promote evolution of constituent species depending on the number of species and the distribution of interaction strengths across the interaction network. Genetic interactions, such as horizontal gene transfer, might also affect evolutionary outcomes. These evolutionary mechanisms in turn affect whole-community properties, such as the level of ecosystem functioning. Successful management of both ecosystems and focal species requires new understanding of evolutionary interactions across whole communities.

1. INTRODUCTION

A major challenge for twenty-first century biology is to understand evolution in complex ecosystems (Liow et al. 2011, Post & Palkovacs 2009, Schoener 2011). How does a community of interacting species evolve in response to a new environment? How do evolutionary responses in turn affect ecosystem properties? These questions have numerous applications—ranging from managing gut bacterial communities for human health (Delzenne et al. 2011) to predicting species responses to climate change (Berg et al. 2010, Munday et al. 2013)—yet current evolutionary and ecological knowledge is insufficient to answer them.

Most theories and experiments on evolutionary dynamics focus on single species. This approach has led to a good understanding of genetic mechanisms of adaptation, but attempts to predict evolution in the wild have met with limited success. One possible reason is that all species live in diverse communities with many hundred or thousand other species present. If ecological dynamics and species interactions alter how each species adapts to change, a single-species approach will be insufficient to predict evolution in diverse systems. For example, adaptation of a bird species to global warming depends not only on genetic variation in the timing of breeding and selection on that trait (Visser 2008) but also on how competing species, insect prey, and the insects' food plants respond to the change, which in turn depends on how the focal bird species adapts (cf. Harmon et al. 2009, Lavergne et al. 2010).

Examples of coevolution between interacting species show that ecological interactions between species can drive evolution when selective forces from biotic interactions shift over space (Geographic Mosaic hypothesis; see Thompson 1999) and time (Red Queen hypothesis, Stenseth & Smith 1984). There is also growing evidence that evolution affects ecological dynamics of single species, pairs of interacting species (Fussmann et al. 2007, Yoshida et al. 2003), and ecosystem properties such as stability and nutrient cycling (Gravel et al. 2011, Urban 2013). However, general theory and evidence for evolution in whole systems is lacking: Many studies still adopt a focal-species approach. Quantitative theory equivalent to the wealth of theory for single populations is lacking.

Below, I review existing theory on how species interactions in diverse communities influence the evolution of component species and the evidence for those theories. My focus is evolution within species over short- to mid-term timescales rather than the longer timescales of speciation and extinction. The ultimate goal is to understand and, if possible, to predict evolutionary dynamics over multiple generations (**Figure 1**). Of particular interest are changes in traits that influence species interactions and determine the match of each species to environmental conditions. I restrict the term evolution to genetic changes within species over time. I refer to changes in the relative abundance of different species within a community as ecological changes or sorting (although note that some authors refer to changes in species abundances as the evolution of a community). After outlining the challenges in conceptualizing and measuring evolution across whole communities, I describe multiple ways in which species interactions can shape evolution in communities. Possible consequences for the functioning of communities and ecosystems are discussed. I then outline future directions that are needed to tackle this hard problem.

2. EVOLUTIONARY DYNAMICS WITH NO SPECIES INTERACTIONS

The baseline scenario for evolution in communities is that species interactions are so weak or inconsistent that they exert negligible selection compared with selection from other sources. If so, species should evolve in parallel to changes in the abiotic environment or reproductive pressures within species irrespective of which other species are present. This scenario has been called the
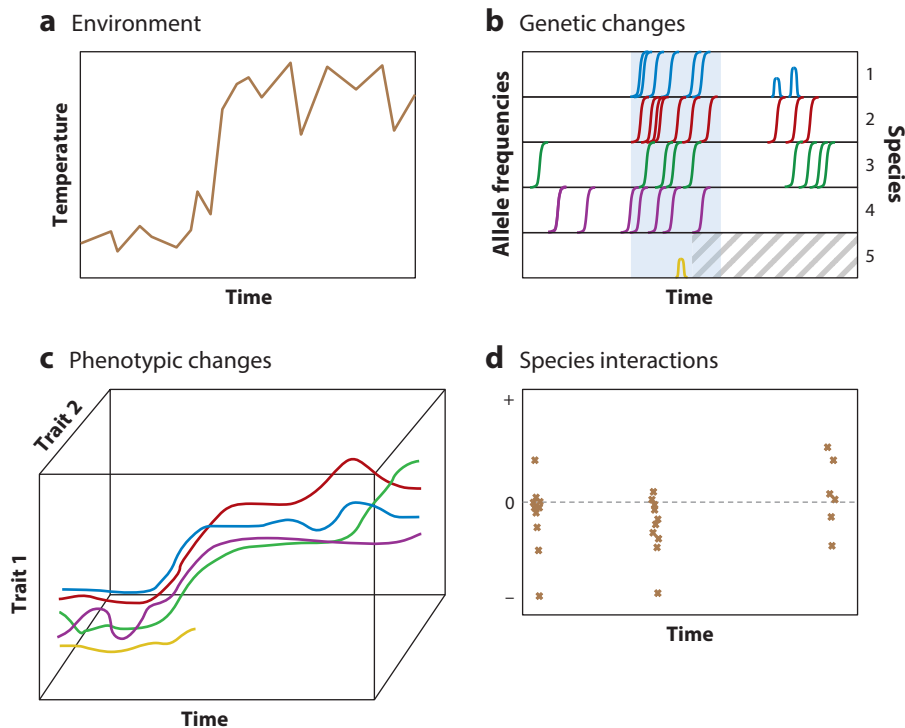
a Environment

b Genetic changes

c Phenotypic changes

d Species interactions

Figure 1

Understanding evolution across whole communities requires knowledge of (*a*) changes in abiotic conditions, (*b*) dynamics of genetic changes across multiple species (colors represent different species), (*c*) changes in phenotypic trait values, and (*d*) the network of species interactions and how it changes over time. In the hypothetical scenario shown, the yellow species fails to adapt and goes extinct. The remaining species evolve and track the environment. They initially converge in resource use (affected by trait 1), leading to more negative species interactions, but diverge in resource use by the end of the time period. The goal of this review is to understand how species interactions influence evolution, in response to both biotic pressures caused by interactions and abiotic pressures caused by environmental change.

Court Jester hypothesis (Barnosky 2001) in relation to macroevolutionary trends in the fossil record (in contrast to the Red Queen hypothesis discussed below). Evolutionary dynamics across whole communities in this scenario can be predicted through the use of standard population genetic theory for single species. Several parameters might vary among species and lead to differences in evolutionary dynamics. I discuss separate effects assuming "all else being equal" in the following, but of course different parameters interact in their effects. A synthetic approach considering multiple factors is needed to predict how different species will respond to a given environmental change.

The expected rate of evolution of a set of quantitative traits per generation is the product of the genetic variance of each trait, the genetic covariance among traits, and the selection pressure acting on each trait (Lande 1979). The first two terms reflect the genetic potential for evolving, and the third term reflects the environmental pressure to evolve. These quantities themselves are influenced by other traits that vary across species and might determine the rate and magnitude of evolution across species in a community over a given time. Because different species have different generation times, the standard equation must also be multiplied by generation time to obtain

comparable rates per time interval. Species with shorter generation times should evolve faster on average than those with longer generation times. This concept is uncontroversial, but there are surprisingly few comparative tests for phenotypic traits (Evans et al. 2012).

In terms of genetic potential for evolution, genetic variance should be higher, on average, in species with larger population sizes and faster mutation rates (Lanfear et al. 2014, Neher et al. 2010). Higher values increase both standing levels of variation through mutation-selection balance and the supply rate of new beneficial mutations. Mutation rates in turn might correlate with other traits such as genome size, number of cell divisions per generation, or metabolic rates (Bradwell et al. 2013). Effects on evolutionary rates are expected to be linear at low values and to saturate as the product of mutation rate and population size, termed θ, increases (Maynard Smith 1976). Different models for trait evolution differ in whether they assume a linear effect of population size (e.g., the canonical equation of adaptive dynamics) or no effect (e.g., quantitative genetics; see Fussmann et al. 2007); these models assume that populations are below or above the saturating point, respectively. If the mutation supply rate is high enough that multiple beneficial mutations are present in the population, species with higher recombination rates should also evolve faster in changing environments (Fisher 1930). Species could vary in reproductive modes, such as clonality and degree of selfing, or in genetic traits, such as the rate of crossing over per meiosis (Burt & Bell 1987, Haddrill et al. 2007).

Species with fewer genetic correlations among any traits that experience selection in opposing directions should evolve faster (Schluter 1996). Alternatively, genetic correlations could speed up evolution if selection acts in matching directions (Chevin 2013). More generally, for a given environmental change, there are certain genetic covariance structures that maximize the rate of evolution; consequently, some species might be more evolvable than others. Evolvable genetic architectures might themselves have evolved in response to earlier periods of selection (discussed further below). Increasing the number of traits under selection might slow down evolution due to the increased chance of genetic covariance (Orr 2000) or selective interference between linked sites.

With respect to environmental pressures driving evolution, the rate of evolution should increase with the rate of change in the environment, up to a threshold above which the change is too great and species go extinct (Burger & Lynch 1995). For a particular change in environment, some species experience stronger selection pressures than others and therefore should evolve more (as long as the rate of environmental change is below the threshold that would drive the population extinct). This depends on ecological tolerance (the width of environment that a phenotype can tolerate) and phenotypic plasticity (the extent to which a given genotype can change its phenotype; see Chevin et al. 2010). There could be opposing effects: If tolerance or plasticity is too high, species experience no selection; if they are too low, species might fail to survive even a small change in environment (Lande 2009, Price et al. 2003). In general, the rate of evolution should increase with the selective advantage of new mutations, primarily because this increases the genetic variance in fitness (Maynard Smith 1976). This depends in part on phenotype–environment interactions as described above but also on genome features that determine the magnitude of phenotypic changes caused by single mutations, which in turn could depend on genome size or the structure of regulatory networks.

The pattern of environmental changes also interacts with traits to determine species responses. For example, rapid fluctuations should cause evolution in species with short generation times but not in species with longer generation times, whereas both sets of species would adapt to slower changes in environment (Lynch & Gabriel 1987). Over longer timescales, the history of selection can affect responses to current changes. Species that evolved under similar selection in the past might possess genetic architectures conducive toward faster evolution in the present, such as a

Table 1 Determinants of evolutionary rates in the absence of species interactions

Determinant	Model	Empirical examples
Generation time	All population genetic models	A survey of body size evolution rates in mammals, scaled for generation times (Evans et al. 2012)
Mutation rate	(Maynard Smith 1976)	Mutator genotypes of bacteria spread in new environments (Giraud et al. 2001)
Population size	(Maynard Smith 1976)	Saturating effect on adaptation in experimental lines of algae (Colegrave 2002)
Recombination rate	(Fisher 1930)	Adaptation to high salt conditions in sexual and asexual yeast lines (Goddard et al. 2005)
Genetic covariance	(Chevin 2013)	Sticklebacks evolve along lines of genetic least resistance (Schluter 1996)
Rate/history of environmental change	(Burger & Lynch 1995)	Evolutionary rescue of yeast populations enhanced by an earlier period of slow environmental deterioration (Bell & Gonzalez 2011)
Ecological tolerance	(Chevin et al. 2010)	*Serratia* that had evolved wide thermal tolerance displayed enhanced initial growth in other novel environments (Ketola et al. 2013)
Phenotypic plasticity	(Lande 2009)	Genetic assimilation of melanin expression downregulation in *Daphnia* exposed to visual predators (Scoville & Pfrender 2010)
History of selection	(Draghi & Whitlock 2012)	The chance of evolving a citrate-using genotype increased following earlier selection on glucose-limited medium (Blount et al. 2012)

predisposition to larger-effect mutations (Draghi & Whitlock 2012). Intrinsic features such as mutation rate, genetic covariances, and ecological tolerance can evolve themselves and might change in response to selection.

The collective dynamics of a community should depend on the distribution of these parameters across species and the relative importance of each parameter on observed amounts of change. More comparative studies are needed, either experimental or observational, to determine evolutionary rates among species and what features correlate with them (**Table 1**). Are responses correlated or uncorrelated across species? What is the distribution of evolutionary rates—are there a few fast-evolving species or a more even distribution? What is the relative importance of genetic versus environmental factors to the observed amount of change?

Some features of ecological networks might correlate with evolutionary dynamics, even if species interactions do not affect evolution. For example, species at lower trophic levels might tend to have larger population sizes, shorter generation times, possibly faster metabolic rates, and perhaps higher mutation rates per unit time; hence, they have greater evolutionary potential compared with species at higher trophic levels (Lewis & Law 2007). This would correlate with the distribution of responses across a food web and have implications for stability and ecological dynamics, but the evolution of each species could still be unaffected by other species.

3. EVOLUTIONARY DYNAMICS AFFECTED BY SPECIES INTERACTIONS

Species interactions can affect evolution in several ways relative to the predictions of the single-species theory outlined in the previous section. Some of these mechanisms have relatively

minor effects by simply changing parameters in the single-species theory, such as population sizes, whereas other mechanisms have more profound effects that require species interactions to be taken into account for modeling evolutionary outcomes.

3.1. Species Interactions Alter Population Sizes and Hence Rates of Evolution

Many species interactions are negative. Species compete for finite resources, and predators and parasites reduce the density of their prey and host species. If increasing diversity tended to reduce the average effective population size across species, species in diverse communities would have lower genetic variation and rates of beneficial mutation per population (Johansson 2008). This could lower the genetic potential for evolution in more diverse communities or in species experiencing stronger negative interactions within trophic networks. Conversely, species that attain higher densities in more diverse communities through positive interactions, such as generalist predators or parasites, might have greater genetic potential for evolution in more diverse communities if the population size effect holds.

Note that this effect does not require major additions to the single-species approach. If we had perfect knowledge of single-species traits and knew the population sizes of each species in the community, we could predict evolution as outlined above without any information on species interactions. The ecological network would determine the distribution of population sizes and therefore the distribution of evolutionary rates, but knowledge of population size would be sufficient for prediction in any one species. Furthermore, evolution would proceed in the same direction as predicted by the single-species approach, albeit it at a different rate.

This hypothesis makes several assumptions that seem obvious but that lack compelling comparative evidence. First, it assumes that population sizes are lower in communities with more species. There is macroecological evidence that average species abundances are lower in communities with more species (e.g., Niklas et al. 2003). However, these relationships come from latitudinal gradients with many other confounding factors that could affect population sizes, making it unclear if species interactions are the causal factor. Biodiversity-functioning experiments show that species abundances in species-rich plots are lower on average than the monoculture abundances of each species (Loreau & Hector 2001). Systematic evaluation of how population sizes scale with species richness among wild communities would be useful.

The second assumption is that genetic variability is lower in smaller populations and in more diverse communities. The evidence is somewhat contradictory. There is comparative evidence that larger census populations have higher effective population sizes as measured by genetic markers (Manier & Arnold 2006), which, combined with evidence for lower population size in more diverse communities described above, supports the assumption. The quantity of interest here, however, is the rate of beneficial mutation and adaptation rather than the variability of neutral markers. Data on beneficial mutation rates are currently restricted to relatively few species, but they do indicate faster adaptive rates with higher effective population size (Gossmann et al. 2012). However, studies have found positive spatial correlations between species diversity and genetic diversity, potentially contradicting the assumption of a negative relationship (Papadopoulou et al. 2011, Vellend & Geber 2005). The nature of relationships among population sizes, genetic diversity, and species diversity remains unresolved.

The final assumption is that evolutionary rates are limited by genetic variation. As argued above, theory predicts that evolutionary rates should saturate with increasing population size; such saturation has been demonstrated with evolution experiments. Observed rates of evolution in nature, however, are easily attainable with measured levels of genetic variation; therefore, genetic variation seems not to be limiting (Barton & Partridge 2000, Hendry & Kinnison 1999,

Lynch 1990). Instead, the rate of change in the environment and ecological opportunity might be the main determinant of observed evolutionary rates (Simpson 1949): Genetic variability of most species may be sufficient to keep pace with changing environments. Some new functions and innovations could be mutation limited, such as the origin of citrate metabolism that evolved after 20,000 generations in long-term selection experiments with *Escherichia coli* (Blount et al. 2012). However, that delay depended on the temporal sequence of earlier mutations and contingency rather than mutation supply rate per se. Whether these events would have happened sooner in larger populations is unclear because the cultures had an effective population size of 3×10^7.

Overall, it is not clear whether conditions are met in order for this mechanism to have a large effect. In any case, as argued above, predictions from single-species theory would be unaltered in attempts to model evolution in a given community. A more interesting consequence of this mechanism would be a kind of evolutionary Allee effect. Smaller populations would be less able to adapt to environmental change and therefore would dwindle further in size, whereas larger populations would adapt faster and increase in size (Johansson 2008). In turn, this could change the network of ecological interactions and evolutionary outcomes in the coevolutionary scenarios discussed further below.

3.2. Ecological Sorting Inhibits Evolution of Constituent Species

Consider a change in abiotic conditions, such as an increase in temperature. One possible response is that all species adapt by evolving to cope with the higher temperature (e.g., evolve enzymes with higher optimal temperatures). Another is that there is an ecological response in the abundance and distribution of the species. Species that were preadapted to grow better at higher temperatures increase in abundance or colonize the region, whereas species that grow better at lower temperatures decline and perhaps go extinct (Fowler & Macmahon 1982). If species compete for limited resources, such ecological sorting might inhibit evolutionary responses of component species (de Mazancourt et al. 2008, Johansson 2008). Species that could have evolved tolerance of higher temperatures in isolation are unable to adapt because they are outcompeted by preadapted species already tolerant of higher temperatures.

De Mazancourt et al. (2008) demonstrated this mechanism in a model of patches connected by dispersal, each with a different optimum value along a single niche axis referred to as temperature (**Figure 2a**). As global temperature increased, species tended to disperse to patches with conditions like their original patches, rather than evolve, even when the same species could adapt to the temperature increase in their original patch in the absence of competition. Theoretically, in some cases evolution was increased because competition increased selection pressure on a given species (Osmond & de Mazancourt 2013), but overall the amount of evolution per species declined as the number of species increased. Johansson (2008) found the same effect in a model of species partitioning a Gaussian resource distribution. When the resource distribution shifted to increasing values, species with resource use furthest from the direction of change declined in abundance and often dwindled to extinction (**Figure 2b**). This occurred both because of a population size effect on evolutionary rate (linear in the equations used) and because of competition from the species that was closer to the changing resource optimum.

The key assumption behind these models is that most trait variation within a community is between species rather than within species, so that selection acts primarily on the relative abundance of different species rather than on the frequency of different genotypes within species. This assumption seems reasonable. Intraspecific variation at most loci tends to be on the order of a few percent at the nucleotide level. Recent work on community genetics emphasizes the importance of genetic variation for ecological interactions (Bolnick et al. 2011) and that there can
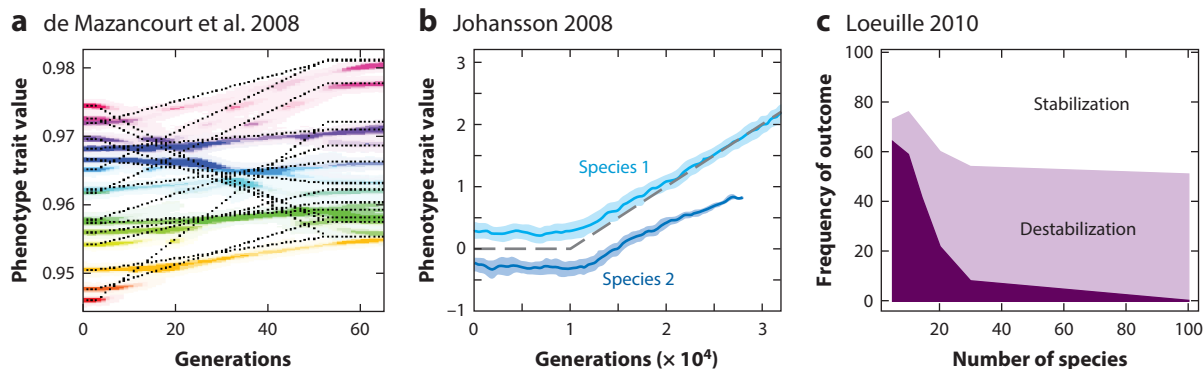
a de Mazancourt et al. 2008 **b** Johansson 2008 **c** Loeuille 2010

Figure 2

Species interactions affect evolution of constituent species, which in turn influences community stability, as shown by three models. (*a*) De Mazancourt et al. (2008) modeled a community of 16 species with phenotypes (*colored lines*) initially specialized on 16 discrete patches with different optimum temperatures (*dashed lines*). Following a global average increase in temperature, species tend to migrate to patches with temperatures matching their initial phenotype rather than evolving. (*b*) Johansson (2008) tracked two species partitioning a Gaussian resource distribution with the mean shown by the dashed gray line. The trailing species 2 fails to keep pace when the mean resource value increases, because it is outcompeted by species 1. (*c*) Loeuille (2010) showed how evolution in turn can alter the stability of communities, especially as the number of species increases. Dark violet indicates frequency of Lotka-Volterra communities with randomly allocated interaction coefficients that showed no effect of evolution on stability; light violet indicates frequency of communities destabilized by evolution; white indicates frequency stabilized by evolution. Graphics adapted from the source papers with permission.

be adaptive polymorphism or ecotypes locally adapted to different environments, but still these are limited compared with between-species variation. Interspecific variation, in contrast, even within a local community, encompasses many millions of years of independent evolution leading to major trait differences and divergence in gene sequence and content.

In addition, the mechanism assumes that there is standing trait variation relevant to new conditions. For an increase in temperature, it assumes that species vary initially in their ability to grow and reproduce at higher temperatures. Such variation could reflect specialization to different local microhabitats or emergence at different times of year. Or species might vary in ecological tolerance and plasticity even if they have the same optimum temperature. Immigration can also bring in species adapted to conditions outside the local region, as shown by de Mazancourt et al. (2008).

A putative example comes from thermal niches of ectotherms. Species tend to vary little in their upper thermal limits but vary much more in lower thermal limits (Sunday et al. 2011). If temperatures were to decline, the ecological sorting mechanism would predict that preadapted species with lower thermal limits would spread whereas other species would be outcompeted and decline to extinction. If temperatures were to increase above the upper thermal limit, only species that evolved higher thermal limits would survive. This would depend on the species' evolvability, namely their intrinsic determinants of genetic variability and genetic covariance.

The assumption that ecological sorting predominates over evolutionary responses is central to paleoecology and niche modeling. Reconstructing past climates on the basis of species presence assumes that abiotic niche characteristics are fixed (Nogues-Bravo 2009). Evidence of phylogenetic niche conservatism also indicates that ecological traits can be highly conserved over long timescales (Peterson et al. 1999). This raises the question of when evolution occurs. Clearly, evolution must happen sometimes, in order to explain ecological differences among species in the first place.

One possibility is that species evolve with the emergence of extreme conditions or completely new resources that are outside the envelope of existing variation (Tilman & Lehman 2001). Which

species would evolve to exploit the new conditions: the most evolvable species (e.g., those with high genetic variability or short generation times), the ecologically dominant species, or the species closest initially to the trait values needed to exploit the new conditions? Alternatively, evolution might occur most readily in unsaturated environments. For example, lupines have radiated into a broad range of plant niches in empty montane habitats formed by the uplift of the Andes, presumably helped by the preadaptation of their northern temperate ancestors to cooler climates (Hughes & Eastwood 2006). Similarly, character displacement of benthic and limnetic sticklebacks occurs only in lakes with a low diversity of other fish (Ormond et al. 2011).

Models of ecological sorting confirm that evolution is more likely in isolated communities that have low ecological heterogeneity and low dispersal (de Mazancourt et al. 2008, Norberg et al. 2012) but that experience environmental changes over time. Then there is insufficient variation among species to permit ecological sorting. Also, regular fluctuation in the environment could erode ecological variation at the extremes of the distribution each time the environment changes, so eventually species that are specialized to extreme conditions would have to re-evolve.

3.3. Species Interactions Stimulate Coevolution

If species adapt to the presence and attributes of other co-occurring species, species interactions might stimulate evolution across communities, even in the absence of abiotic change. This is the tenet of the Red Queen hypothesis (Liow et al. 2011). Biotic interactions with mutualists, competitors, predators, and prey exert strong selection on species. Furthermore, the strength and direction of selection varies over time and space either because the composition of co-occurring species changes (Thompson 1999) or because of reciprocal coevolutionary change in interacting species (Stenseth & Smith 1984). Increasing the number of interactions could multiply the number of selection pressures acting on populations and increase the complexity and, potentially, the unpredictability of evolutionary outcomes (Benkman 2013). I focus here solely on the effects of biotic interactions, and in the next section I explore how coevolution could in turn affect responses to abiotic change.

The dynamics of reciprocal coevolution between pairs of species with strong interactions are well known (Abrams 2000, Case & Taper 2000). One outcome is that species evolve toward a new equilibrium state to reduce the strength of negative interactions between them—for example, when competing species evolve niche partitioning. This would not drive ongoing evolution unless community composition or resources were to fluctuate over time. For example, Lawrence et al. (2012) showed that a community of four bacterial species evolved divergent resource use. Species interactions were more positive between evolved lines than between ancestral isolates or between the same species evolved in monoculture (**Figure 3a**). Positive interactions were explained by cross-feeding interactions: Species evolved to use waste products of other species, as demonstrated by chemical analysis. Changes in interactions were consistent among different replicates, indicating that species evolved toward similar patterns of resource use repeatedly, rather than in different directions. Nonetheless, resource use evolved more in communities than in monocultures faced with the same abiotic conditions.

An alternative outcome of coevolution is an arms race between species to maximize their benefits from interaction and minimize the costs (Abrams 2000). Predators evolve better prey detection and consumption mechanisms, whereas prey evolve better antipredator defenses. For example, simulations of digital organisms following predator–prey interactions determined by simple genetics yielded a coevolutionary dynamic of predators evolving to exploit the most common prey, followed by prey evolving resistance to the most common predator (Bell 2007). Arms race dynamics are known in coevolving bacteria and bacteriophage (Gomez & Buckling 2011)
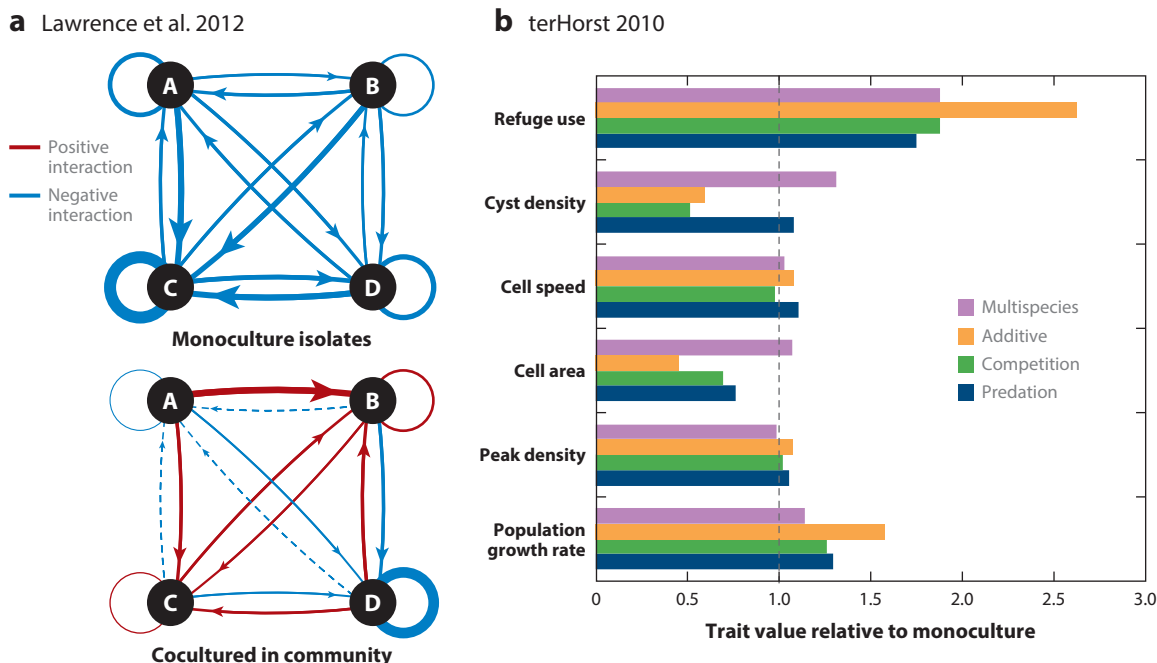
Figure 3

Species interactions stimulate and alter the direction of evolution. (*a*) Four bacteria species (A, B, C, D) evolved more positive interactions (*red, thicker lines*: stronger effects; *dashed lines*: insignificant effects) when cocultured in a community compared with negative interactions (*blue lines*) between isolates that evolved separately in monoculture. Panel *a* modified from Lawrence et al. (2012). (*b*) Traits of the ciliate *Colpoda* sp. from the pitcher plant inquiline community evolved differently in the presence of predation (mosquito larvae), competition (another ciliate), or a multispecies community including all three species. Traits in the multispecies treatment (*purple bars*) evolved to be closer to monoculture trait values (indicated by a value of 1) than expected if competition and predation had additive effects (*orange bars*). Panel *b* displays data from terHorst (2010).

and animal–parasite systems (Decaestecker et al. 2007). In mutualisms, there might be selection for traits that maximize benefit and minimize the costs of engaging with the partner (Login et al. 2011).

In diverse communities, pairwise coevolution might be constrained by the network of multiple interactions. Species could evolve traits for coping with generic biotic interactions, such as insect herbivory, rather than for interacting with a particular species. Coevolution might occur only when specialists interact with few other species (i.e., species with the fewest, strongest links rather than species with many weak links). Alternatively, coevolution might occur among multiple interaction links, perhaps even propagating evolution through the network. Guimarães et al. (2011) modeled coevolution in a mutualistic network and found that coevolution increased evolutionary rates (compared with models excluding coevolution) but that coevolution was constrained by the presence of supergeneralist species that interact with many other species.

Several recent experiments found that coevolution is constrained or altered by the presence of a diverse background community. Coevolution between *Pseudomonas fluorescens* and bacteriophage shifted from an arms race dynamic when cultured alone to a fluctuating selection dynamic (i.e., hosts became more resistant to contemporary bacteriophage than to past or future bacteriophage) when cultured with a soil community present (Gomez & Buckling 2011). Similarly, several traits of the ciliate *Colpoda* evolved in response to mosquito predation and competition from another

ciliate when exposed to each in turn (**Figure 3b**), but monoculture traits were retained when the ciliate was cultured with both mosquitos and protozoan competitors simultaneously (terHorst 2010). This was consistent with greater species diversity constraining adaptation to the presence of both predators and competitors.

In part, the strength of coevolution should depend on the consistency of community composition. Closed communities that retain the same set of species over extended times provide the opportunity for species to adapt with particular species. Again, therefore, communities closed to immigration provide the best conditions for promoting evolution versus ecological changes. Oceanic islands are both depauperate of competing species and closed regions with limited immigration through dispersal. Microcosm experiments could test whether low diversity or consistency of co-occurring species best explains striking patterns of evolution on islands.

3.4. Interference Between Adaptation to Biotic and Abiotic Environments

Adaptation to co-occurring species might affect adaptation to the abiotic environment and vice versa. If so, evolutionary responses to a given abiotic change could depend on which other species are present. For example, *Daphnia magna* evolved a faster intrinsic growth rate in monocultures exposed to a 4°C increase in temperature but evolved smaller size at maturity when faced with the same change in mesocosms containing competitors, predators, and parasites (Van Doorslaer et al. 2010). This effect is consistent with trade-offs between optimum phenotypes for abiotic versus biotic environments. For example, reduced adaptation to elevated CO_2 levels in multigenotype algal cultures versus monocultures was attributed to a trade-off between CO_2 adaptation and competitive ability (Collins 2011). Investment in costly defense traits could also reduce the energy available for investment in other traits (Loeuille 2010), as supported by a trade-off between growth and defense in Amazonian plants (Fine et al. 2006). Increased dimensionality of the environment might increase the chance of selective interference between traits. Alternatively, standing variation maintained by spatially or temporally variable biotic interactions might enhance adaptation to new biotic or abiotic conditions. For example, plants from species-poor communities might harbor lower standing variation for defensive and competitive traits needed to adapt to an invasive species (Leger & Espeland 2010).

Species interactions could also augment the effects of abiotic changes by propagating evolutionary responses through an ecological network. Northfield & Ives (2013) showed that interactions either amplified or dampened the effects of environmental change on species abundances and extinction in Lotka-Volterra models when coevolution was either nonconflicting (e.g., niche partitioning) or conflicting (e.g., arms race in competitive ability), respectively. In the model of Guimarães et al. (2011) described in the previous section, evolution under their parameter values occurred primarily as background evolution to abiotic change rather than coevolution. To test these ideas, general surveys are needed that partition the relative strength of biotic and abiotic selection pressures across species of a community and that determine how often arms race dynamics occur. Species interactions might also increase evolutionary responses to abiotic conditions by strengthening selection pressures (Osmond & de Mazancourt 2013). For example, selection for earlier flowering in *Arabidopsis thaliana* at elevated CO_2 levels was 50% greater in the presence of a competing grass species (Lau et al. 2014).

3.5. Gene Transfer Might Facilitate Evolution in More Diverse Communities

If transfer of genetic material between species plays a role in adaptation, evolution might be affected by genetic interactions between species as well as ecological interactions. In prokaryotes, gene

transfer could occur via a range of mechanisms either by homologous recombination or by vectors like plasmids and viruses. In eukaryotes, it could occur via hybridization or rare incorporation of foreign DNA by other means. To understand evolution involving genetic interactions among species, we would need to know the network of potential spread via different mechanisms, the types of genes that can be transferred into new backgrounds, and the ecological consequences of transferring a trait.

Horizontal gene transfer (HGT) is a well-known mechanism for acquiring new functions in microbes (Ochman et al. 2000). It could also potentially influence dynamics of adaptation to changing conditions over short to medium evolutionary timescales. Some bacteria take up DNA and incorporate it into their genomes by transformation. The probability of recombination generally declines with increasing sequence divergence. A rare nonhomologous recombinant genome spreads only if the foreign DNA is compatible with the genomic background and if it conveys a selective advantage (Novozhilov et al. 2005). Beneficial HGT events might therefore be more likely in diverse communities if the availability of compatible donor and recipient genomes is limiting and between more ecologically similar species in which transferred genes are more likely to be beneficial (Smillie et al. 2011).

HGT can also occur via a vector such as a plasmid (conjugation) or a virus (transduction). These often transfer multiple genes and confer a new function such as antibiotic resistance and heavy metal tolerance. Not all donor–recipient transfers are possible, however. A recent meta-analysis found that half of plasmids identified from genome data were not mobilizable and the remainder tended to group within defined clades (Smillie et al. 2011). On average, the probability of a successful HGT might again increase with species richness. Because vectors are under selection to spread independently of host genomes, there could be complex interactions between the ecological impacts and the evolutionary benefits of HGT vectors (Harrison & Brockhurst 2012). For example, competition between coexisting plasmids or hosts could generate selection for reduced HGT rates (Haft et al. 2009).

HGT has different effects from mutation within genomes. It creates new trait combinations by bringing together genes from different genomes. Larger phenotypic shifts in which species acquire a new function with a single event are possible. Also, species can acquire traits from other species, changing ecological interactions between donor and recipient species. Acquisition of an alpha niche trait such as a gene for metabolizing a new resource would cause the recipient to expand its niche, leading to increased niche overlap with the donor (Wiedenbeck & Cohan 2011). Selection might act against HGT in this case by favoring different conjugation mechanisms or reduced DNA secretion (Draghi & Turner 2006). Acquisition of a beta niche (environmental filter) trait allows a species to invade a new habitat or survive a major change in its own habitat. Most documented cases of HGT fall into this category. Examples include antibiotic resistance and pathogenicity genes—HGT scenarios with strong selection in which only species with a particular trait can invade (Barraclough et al. 2012).

It is unclear, however, what role HGT plays in microbial adaptation over short to medium timescales. Most evidence comes from retrospective studies of genome sequences (Smillie et al. 2011). Acquisition of new metabolic functions in *E. coli* has been attributed entirely to HGT (Pál et al. 2005), but these events affected 16 kb every one million years (Lawrence & Ochman 1998), which is only 10% of the rate of nucleotide substitutions (Barrick et al. 2009). Experimental studies mostly screen trillions of cells for antibiotic resistance, rather than follow evolution of populations in natural conditions (Thomas & Nielsen 2005). We need experiments of mixed cultures that quantify HGT and manipulate it (Perron et al. 2012). Recent work has documented HGT during colonization of acid mine drainage over several decades (Denef & Banfield 2012) (**Figure 4**), raising the possibility of tracking HGT over experimental timescales in field populations.
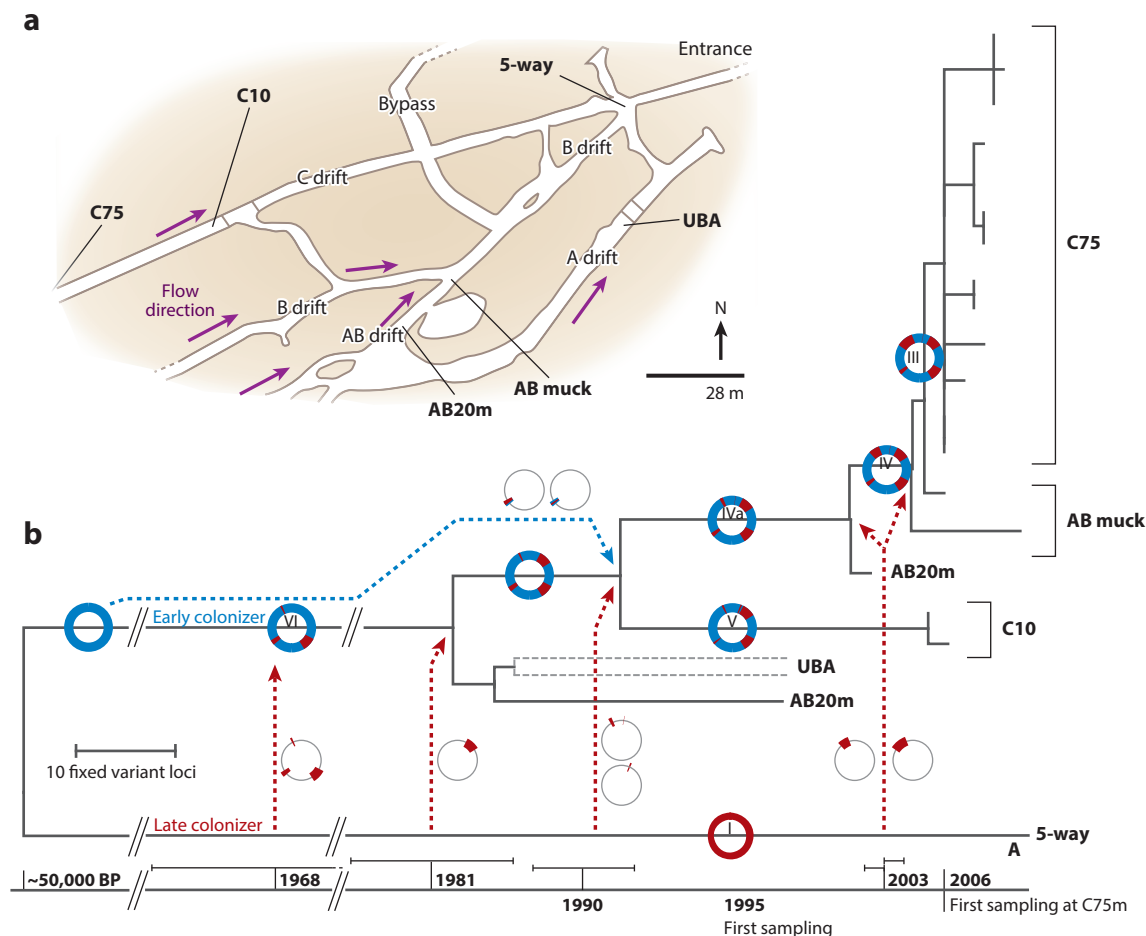
Figure 4

Horizontal transfer and nucleotide substitutions contribute to bacterial adaptation. Two genetically distinct ancestral strains of *Leptospirillum* group II bacteria colonized acid drainage of the Richmond Mine in northern California. (*a*) Sampling localities in the mine. (*b*) Whole-genome sequencing allowed reconstruction of repeated transfer of segments from one colonist (*red genome circle* and *red dotted arrows* show transfers) to the other (*blue genome circle*) over a period of decades. This led to a progression of genome types classified by Roman numerals. Further substitutions occurring along lineages are represented by the lengths of branches on the phylogenetic tree. Statistical analyses indicated that selection acted on genotypes that differed by just a few nucleotides; hence, both substitution and horizontal gene transfer contributed to adaptation in the mine. Abbreviations: BP, before present; sampling locality codes shown in panel *a*. Figure modified from Denef & Banfield (2012) with permission.

In eukaryotes, hybridization can either transfer adaptations between species (Brand et al. 2013, Hedrick 2013), such as the spread of warfarin resistance between mice species (Song et al. 2011), or create new phenotypes that thrive in novel environments, as in hybrids of Louisiana irises (Arnold et al. 2012). Hybridization as a genetic species interaction could therefore enhance evolution in some circumstances. However, gene flow can also limit evolution via the influx of maladapted genes or genetic homogenization of formerly separate species (Seehausen et al. 2008). Incorporation of foreign DNA also contributes to new adaptations, such as carotenoid production in aphids using fungal genes (Moran & Jarvik 2010) and galactomannan metabolism in coffee berry borers using a bacterial gene (Acuna et al. 2012). Recent estimates of HGT found relatively high levels in some

animals (Boschetti et al. 2012), comparable with early estimates for bacteria (Ochman et al. 2000). However, again, it is unclear whether HGT would have a large effect on adaptation to background environmental change versus the rare acquisition of new functions.

4. CONSEQUENCES FOR COMMUNITIES AND ECOSYSTEMS

The mechanisms described above have consequences in turn for how evolution affects functioning of whole communities. Recent work shows how evolution of focal species can affect food web structure (Harmon et al. 2009, Pantel et al. 2011) and ecosystem processes (Lennon & Martiny 2008). Also, communities constructed with species that were evolved to be more generalist or specialist showed how evolutionary history can affect biodiversity–ecosystem functioning relationships (Gravel et al. 2011). But how does evolution across whole communities affect properties such as community stability or nutrient flow?

Evolution might often be expected to enhance ecosystem functioning. If new functions that were not present initially evolve, or if specialization and niche partitioning lead to complementary resource use among species, the whole community might use resources more efficiently or completely. For example, in the study by Lawrence et al. (2012), niche partitioning and cross-feeding evolved in laboratory cocultures of four bacteria species and led to enhanced productivity that was measured as the respiration rate of the whole community.

Alternatively, evolution might reduce community functioning if some species evolve to monopolize resources or otherwise destabilize the community. Which outcome occurs could depend on several factors. For example, Loeuille (2010) found that evolution of interaction strengths mainly enhanced or did not change the stability of Lotka-Volterra communities with fewer than 30 species but either reduced or enhanced stability with equal frequency in more diverse communities (**Figure 2c**). The effect varied among interaction types: Stabilization was strongest for trophic and mutualistic interactions and weakest for competitive interactions. It was associated with the emergence of many weak and few strong trophic interactions. Larger communities were more frequently destabilized than smaller ones because of the increased chance that new mutant phenotypes would affect the population density of more species. Although more diverse communities had greater species turnover and dynamic instability, whole-network properties were conserved (see also Bell 2007, Caldarelli et al. 1998, Christensen et al. 2002) because of functional redundancy of traits and network features. Evolution might also shift ecosystem processes to alternative states. For example, in the work of Matthews et al. (2011), allowing resource uptake rates of primary producers to evolve in a model of ecosystem dynamics altered nutrient cycling and the ratio of producer and consumer biomass.

Another possible effect is that evolution restores functions lost by species extinction. Environmental change can cause species extinction and an associated decline in functional diversity. Recovery of ecosystem functioning depends on whether species performing the lost function can invade from elsewhere or whether surviving species can evolve the lost function. Tilman & Lehman (2001) modeled a community that partitioned a niche axis and was affected by environmental change. Only a subset of species survived, and the survivors subsequently diversified to occupy empty niches. Whether evolution ameliorates the effects of anthropogenic extinctions on ecosystem functioning depends on timescales. The observed recovery time for taxonomic diversity following mass extinction events was around 2 to 9 million years, but functional diversity might recover more quickly (Chen & Benton 2012).

In theory, selection could sometimes act at the level of whole communities for enhanced functioning (Boyle et al. 2012, Williams & Lenton 2008). For example, host-associated microbiota such as termites' gut bacteria are vital for breaking down indigestible polymers in host food.

Functioning within the community depends on the joint action of many species, which includes intimate mutualisms between protists and bacteria, and microbial composition is conserved within termite genera (Hongoh et al. 2005). Better functioning communities enhance host fitness and might increase the chance of being transferred to new hosts, either vertically or horizontally. Evidence of optimal functioning or complementary functions of species is not sufficient evidence that selection acts at the community level, however. Complementary functioning can also arise as a by-product of ecological assembly or selection on constituent species and, as argued above, individual selection can disrupt functioning. Experiments that artificially select communities for particular functions could be used to test these ideas.

5. FUTURE DIRECTIONS AND CHALLENGES

The above mechanisms likely apply simultaneously to different species in a community. Even the scenario in which species interactions have little effect on evolution outlined in Section 3 has a vast number of parameters for communities of realistic size: The complexity is magnified further if species interactions do affect the outcomes. How can we hope to understand the properties of systems depending on so many parameters? Perhaps the first step is to establish which features of species and interactions generate particular outcomes in theory and to test predicted trends rather than a precise formulation of the entire system.

5.1. Mathematical Models of Evolutionary Interactions Across Communities

Ecological interactions among species can dampen evolution of component species through reduced population size or ecological sorting (Sections 3.1 and 3.2), stimulate evolution through coevolution (Section 3.3), and/or alter evolutionary outcomes by changing selection pressures relative to abiotic conditions alone (Section 3.4). Mathematical models of whole communities that contain realistic ecological interactions and evolution are now needed to understand the conditions that promote each mechanism. How do processes vary with the number and type of species, distribution of interaction strengths, and levels of immigration?

The gold standard for evolutionary models is a tractable system with analytical solutions. Whole-community models are messy and require simulation approaches to identify trends. However, by taking slices through parameter space or running replicates with a distribution of input parameters, we can gain a general understanding of behavior. Many existing models of species interactions are hard to compare with empirical data, as interaction strengths are coded through the use of coefficients that are difficult to measure. Existing models assume one-dimensional environments and phenotypes that greatly simplify specification of organisms' interactions with their environment. Dynamics might differ, however, depending on whether environmental change is parallel to or orthogonal to niche partitioning axes.

One promising approach for simplifying and connecting to empirical tests is to develop mechanistic models. Instead of incorporating interaction strengths that require measurements for each pair of species, underlying traits and resource use of each species are modeled and interactions and selection pressures are derived from patterns of complementarity or overlap. For example, ecological models of trophic webs specify vital rates determined by allometries with body size; species interactions are then derived from body size rules [e.g., predators only eat prey within a certain size range (Berlow et al. 2009)].

Another promising case where a mechanistic underpinning is within reach is in microbial communities. Microbial resource use is structured to a large degree by metabolism. Species that metabolize the same compounds compete, and species that use other species' waste products

(cross-feeding) are facilitated. Species interactions can be predicted on the basis of enzyme content inferred from genomes (Bomar et al. 2011). Human gut bacteria with more similar metabolism as predicted from metagenomic sequences are more likely to co-occur, consistent with the concept of habitat filtering based on resource availability (Levy & Borenstein 2013). These approaches could be combined with models of the evolution of metabolism in populations (Herron & Doebeli 2013, Pfeiffer & Bonhoeffer 2004) to predict how the network of species interactions affects evolution in response to changing resource availability. Is evolution restricted to a few species or do all species tend to evolve when resources change, perhaps with evolution propagated through the interaction network?

Another general issue is how to code evolution. Some models adopt an Evolutionary Stable Strategy approach and look at invasibility criteria of genotypes with new properties. In effect, these are ecological models looking at how stable a community is to the immigration of new species— they lack a clear separation between within-species evolution and between-species ecological changes (Lewis & Law 2007). Also, although equilibrium state is important, communities are in permanent transience if the environment or species interactions change frequently. Models that incorporate mutational change to phenotypes within each species, such as quantitative genetics or adaptive dynamics for quantitative traits (Fussmann et al. 2007), and that contain parameters that can be measured experimentally are needed. The question of how genetic interactions via HGT or hybridization affect evolution in whole communities remains wide open. Models with stochastic transfer of genetic traits between species are needed. Although there are models of plasmid transfer, few have looked at the combined dynamics of multiple host and donor populations of bacteria transferring a trait (Haft et al. 2009).

5.2. Surveys of Evolutionary Dynamics in Whole Communities

Many questions raised in this review can be answered only by empirical surveys of evolution in whole communities. What are the main determinants of evolutionary rates? When the environment changes, what kinds of species evolve more and what kinds evolve less? Do the rate, direction, and amount of evolution depend more on intrinsic genetic features or on the pattern of environmental change and ecological opportunity (Mahler et al. 2010)? Current evidence mostly considers noninteracting species across separate environments.

Collecting suitable data for plant and animal communities is hard. Species interactions vary over time and are difficult to measure experimentally. Interaction networks can be inferred from field surveys of predation or pollination (Elias et al. 2013), but even this is time consuming. Measuring evolution is also difficult. Changes in mean trait values depend on demography and plasticity as well as genetic changes (Ozgul et al. 2009), and the genomic variation underlying adaptive traits is unknown in most species. Most studies of animals and plants infer selection over very few generations, rather than measure evolution over the multiple generations needed to track coevolutionary dynamics (but see Decaestecker et al. 2007). Aquatic plankton, however, offer the advantages of fast generation time, the option to store genotypes between time points for comparison, and the ability to link field results to controlled laboratory experiments (Van Doorslaer et al. 2010).

Perhaps progress in eukaryotes must sacrifice detail for scale. It may be impossible to measure every parameter thought to be important for determining evolutionary responses. Instead, a subset of quantities could be measured (e.g., population sizes, diet through the analysis of stomach contents, trait heritabilities in a subset of species). Observed responses could then be compared with computer models making different assumptions about the distribution of missing parameters. Alternatively, existing focal-species studies could be expanded to include more of the whole

community (Siepielski & Benkman 2010). If interactions are compartmentalized, understanding could come from detailed study of a few species.

Some studies have manipulated field conditions and then observed responses in a few key traits across the community. Long-term experiments like the Park Grass experiment have observed adaptation on adjacent plots experiencing different nutrient treatments for more than 100 years (Freeland et al. 2010). In a similar experiment of more than 20 years, *Rumex acetosa* evolved slower growth rates in field plots protected from predation by rabbits, although their competitive interactions with other plant species did not change as a result (Turley et al. 2013). One issue for field experiments is distinguishing in situ evolution from colonization of preadapted genotypes from outside the experimental site. Colonization by preadapted genotypes blurs the distinction between evolutionary and ecological responses, especially if genotypes belong to different ecotypes of a species. One solution is to compare the dynamics of open and artificially closed systems, in which only in situ evolution and ecological sorting can occur (Van Doorslaer et al. 2010). Of course, it is possible that changes in the wild always involve colonization of preadapted forms from elsewhere and that closed systems are artificial.

With sufficiently resolved fossil records, it is possible to track the dynamics of morphology and inferred niche use over longer timescales and fit models with biotic versus abiotic drivers. Recent work analyzed macroevolutionary rates in planktonic foraminifera—arguably the best resolved fossil record thanks to broad geographical ranges and representation in marine sediments. Speciation rates increased with lower diversity (i.e., reduced species interactions), whereas extinction rates depended more on abiotic conditions (Ezard et al. 2011) (**Figure 5**). Similar analyses could be performed on rates of anagenetic evolution. One challenge is to track changes over medium timescales of, say, 10,000 generations—too long to follow experimentally in most cases, but too short for most fossil records. The recovery of *Daphnia* and other organisms from resting stages in sediment cores permits laboratory experiments and multiyear changes to be linked to medium timescales (Decaestecker et al. 2007).

5.3. Experimental Evolution in Microbial Communities

Microbes present a major challenge for studying evolution in the wild. Because of their great diversity and the difficulty of tracking genotypes in longitudinal studies, there is still little evidence of whether bacteria evolve as rapidly in soil and water as they do in laboratory monocultures or as pathogens. Evolution might be swamped by the colonization of preadapted forms from the rain of spores. A few studies have begun using metagenomics to track changes in genotypes of related species over time (Denef & Banfield 2012). Many current metagenomic studies take static snapshots of diversity across multiple sites; however, more experimental manipulations of microbial communities and tracking changes over time are needed for us to understand population dynamics of bacterial communities.

The greatest potential for uncovering evolutionary mechanisms comes from laboratory experiments. Experimental evolution now needs to embrace the diversity of life and go beyond few-species systems to explore evolution of communities seeded from the wild. Parallel monoculture experiments can be used to quantify the genetic potential of different species to adapt to a wide range of conditions, and these findings can be compared with the species' actual evolution when cultured in diverse mixtures. There are high-throughput techniques for quantifying resource use based on metabolism (Bomar et al. 2011, Lawrence et al. 2012), which is far simpler than quantifying complex resource use of many plants and animals. Individual resource use relates closely to metabolic functioning of whole communities, making these systems ideal for testing whether selection promotes or disrupts ecosystem functioning.
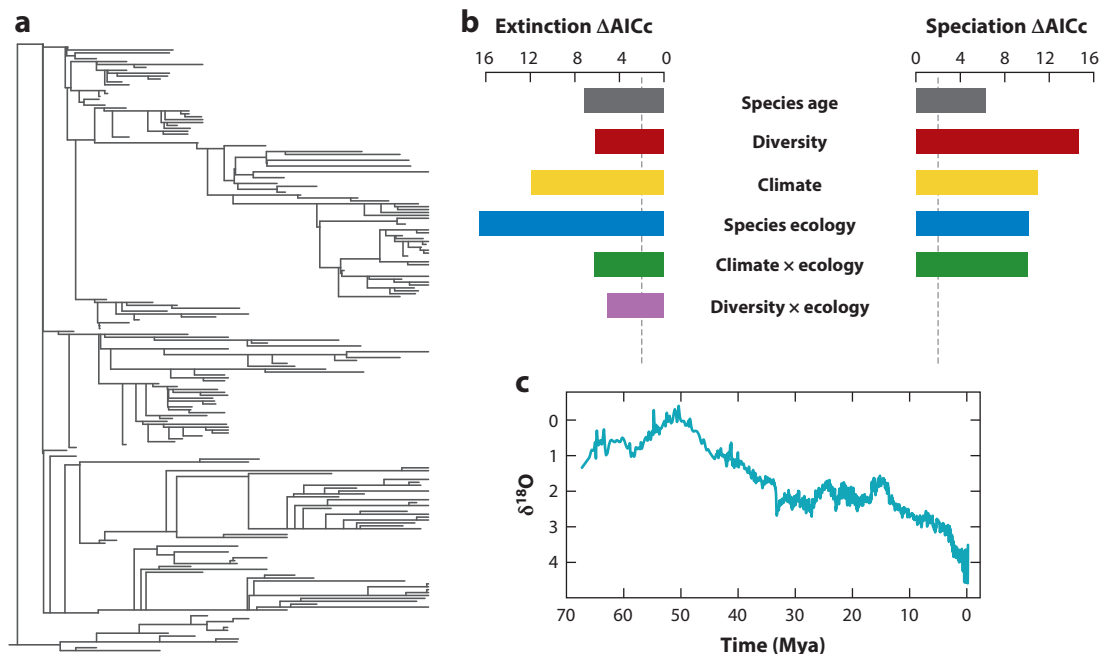
Figure 5

Species interactions influence speciation rates in the fossil record. (*a*) A lineage phylogeny of planktonic foraminifera was reconstructed from fossil evidence. (*b*) Models were fitted to explain per lineage speciation and extinction rates based on a series of variables [summarized here, terms with a change in corrected Akaike information criterion (AIC) of which two were included in the model], such as (*c*) a proxy of global temperatures (inversely related to $\delta^{18}O$, the ratio of ^{18}O to ^{16}O in carbonate sediments). Speciation rates increased when diversity was lower; this finding was interpreted as reflecting ecological opportunity unconstrained by competition from other species. Extinction rates depended more on abiotic conditions and species ecology (habitat and morphology). Figure adapted from Ezard et al. (2011) with permission.

The main challenge is to track abundances and evolution of multiple species in real time. Abundances can be tracked using DNA markers, recognizable phenotypes (limited to a few species; see Lawrence et al. 2012), or fluorescent labels (the most accurate method but currently limited to few-species systems; see Hekstra & Leibler 2012). Evolution can now be tracked by sequencing genomes (Blount et al. 2012) or community metagenomes (although this has rarely been used for temporal dynamics). Genetic changes can be identified from whole-genome sequences at the start and the end of an experiment, and their spread can be recorded in high resolution retrospectively from frozen samples to infer selection (Chubiz et al. 2012). The difficulty, however, is to connect genetic changes with phenotypic effects and sources of selection. Minot and colleagues (2013) tracked genetic changes in viruses infecting human gut bacteria over 2 years and, by virtue of the known mechanism of bacterial resistance, inferred the spread of a mutant virus evading bacterial resistance from sequence data alone. However, the effects of detected changes will not often be so well understood. Most organisms are not tractable for genetic modification to test the phenotypic consequences of a genetic variant: Progress with whole communities might be possible only with lower standards of functional inference than those required for model organisms. Alternatively, species can be isolated to compare evolved versus ancestral phenotypes. For a community of several hundred species, this would require brute force isolation of colonies and genotyping to pick out

each species (Goodman et al. 2011). The solutions to these issues will be major innovations in the coming years.

6. CONCLUSIONS

Understanding evolution across whole communities is a hard problem. But this is the raw material that biologists face, and it is our job to try and make sense of it. The research paradigm for studying evolution has focused on uncovering mechanisms in detail for single species. We now need theory, observation, and experiments across whole communities to understand how species interactions influence evolutionary outcomes. The biggest test will come from attempting to predict and alter outcomes. Treating bacterial infections with antibiotics requires understanding of effects on the functioning of commensal microbiota and whether any alternative strains are preadapted or will evolve to fill the niche left empty by control. Similarly, controlling crop pests while retaining ecosystem services of pollinators and natural enemies requires understanding of how ecological and evolutionary effects of intervention propagate through communities. Clearly, predictability of complex, stochastic systems will be severely limited. Even if detailed outcomes cannot be predicted, however, it might be possible to narrow down and engineer broad alternative outcomes. Solving these problems is required for the future success of evolutionary applications in many areas.

DISCLOSURE STATEMENT

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LITERATURE CITED

Abrams PA. 2000. The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* 31:79–105

Acuna R, Padilla BE, Florez-Ramos CP, Rubio JD, Herrera JC, et al. 2012. Adaptive horizontal transfer of a bacterial gene to an invasive insect pest of coffee. *PNAS* 109:4197–202

Arnold ML, Ballerini ES, Brothers AN. 2012. Hybrid fitness, adaptation and evolutionary diversification: lessons learned from Louisiana irises. *Heredity* 108:159–66

Barnosky AD. 2001. Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *J. Vertebr. Paleontol.* 21:172–85

Barraclough TG, Balbi KJ, Ellis RJ. 2012. Evolving concepts of bacterial species. *Evol. Biol.* 39:148–57

Barrick JE, Yu DS, Yoon SH, Jeong H, Oh TK, et al. 2009. Genome evolution and adaptation in a long-term experiment with *Escherichia coli*. *Nature* 461:1243–74

Barton N, Partridge L. 2000. Limits to natural selection. *BioEssays* 22:1075–84

Bell G. 2007. The evolution of trophic structure. *Heredity* 99:494–505

Bell G, Gonzalez A. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* 332:1327–30

Benkman CW. 2013. Biotic interaction strength and the intensity of selection. *Ecol. Lett.* 16:1054–60

Berg MP, Kiers ET, Driessen G, van der Heijden M, Kooi BW, et al. 2010. Adapt or disperse: understanding species persistence in a changing world. *Glob. Change Biol.* 16:587–98

Berlow EL, Dunne JA, Martinez ND, Stark PB, Williams RJ, Brose U. 2009. Simple prediction of interaction strengths in complex food webs. *PNAS* 106:187–91

Blount ZD, Barrick JE, Davidson CJ, Lenski RE. 2012. Genomic analysis of a key innovation in an experimental *Escherichia coli* population. *Nature* 489:513–18

Bolnick DI, Amarasekare P, Araujo MS, Burger R, Levine JM, et al. 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26:183–92

Bomar L, Maltz M, Colston S, Graf J. 2011. Directed culturing of microorganisms using metatranscriptomics. *mBio* 2:e00012-11

Boschetti C, Carr A, Crisp A, Eyres I, Wang-Koh Y, et al. 2012. Biochemical diversification through foreign gene expression in bdelloid rotifers. *PLOS Genet.* 8:e1003035

Boyle RA, Williams HTP, Lenton TM. 2012. Natural selection for costly nutrient recycling in simulated microbial metacommunities. *J. Theor. Biol.* 312:1–12

Bradwell K, Combe M, Domingo-Calap P, Sanjuan R. 2013. Correlation between mutation rate and genome size in riboviruses: mutation rate of bacteriophage Qβ. *Genetics* 195:243–51

Brand CL, Kingan SB, Wu LJ, Garrigan D. 2013. A selective sweep across species boundaries in *Drosophila*. *Mol. Biol. Evol.* 30:2177–86

Burger R, Lynch M. 1995. Evolution and extinction in a changing environment—a quantitative-genetic analysis. *Evolution* 49:151–63

Burt A, Bell G. 1987. Mammalian chiasma frequencies as a test of two theories of recombination. *Nature* 326:803–5

Caldarelli G, Higgs PG, McKane AJ. 1998. Modelling coevolution in multispecies communities. *J. Theor. Biol.* 193:345–58

Case TJ, Taper ML. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* 155:583–605

Chen ZQ, Benton MJ. 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nat. Geosci.* 5:375–83

Chevin L-M. 2013. Genetic constraints on adaptation to a changing environment. *Evolution* 67:708–21

Chevin L-M, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLOS Biol.* 8:e1000357

Christensen K, de Collobiano SA, Hall M, Jensen HJ. 2002. Tangled nature: a model of evolutionary ecology. *J. Theor. Biol.* 216:73–84

Chubiz LM, Lee MC, Delaney NF, Marx CJ. 2012. FREQ-Seq: a rapid, cost-effective, sequencing-based method to determine allele frequencies directly from mixed populations. *PLOS ONE* 7:e47959

Colegrave N. 2002. Sex releases the speed limit on evolution. *Nature* 420:664–66

Collins S. 2011. Competition limits adaptation and productivity in a photosynthetic alga at elevated CO_2. *Proc. R. Soc. B* 278:247–55

de Mazancourt C, Johnson E, Barraclough TG. 2008. Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* 11:380–88

Decaestecker E, Gaba S, Raeymaekers JAM, Stoks R, Van Kerckhoven L, et al. 2007. Host-parasite 'Red Queen' dynamics archived in pond sediment. *Nature* 450:870–73

Delzenne NM, Neyrinck AM, Backhed F, Cani PD. 2011. Targeting gut microbiota in obesity: effects of prebiotics and probiotics. *Nat. Rev. Endocrinol.* 7:639–46

Denef VJ, Banfield JF. 2012. In situ evolutionary rate measurements show ecological success of recently emerged bacterial hybrids. *Science* 336:462–66

Draghi JA, Turner PE. 2006. DNA secretion and gene-level selection in bacteria. *Microbiology* 152:2683–88

Draghi JA, Whitlock MC. 2012. Phenotypic plasticity facilitates mutational variance, genetic variance, and evolvability along the major axis of environmental variation. *Evolution* 66:2891–902

Elias M, Fontaine C, van Veen FJF. 2013. Evolutionary history and ecological processes shape a local multilevel antagonistic network. *Curr. Biol.* 23:1355–59

Evans AR, Jones D, Boyer AG, Brown JH, Costa DP, et al. 2012. The maximum rate of mammal evolution. *PNAS* 109:4187–90

Ezard THG, Aze T, Pearson PN, Purvis A. 2011. Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* 332:349–51

Fine PVA, Miller ZJ, Mesones I, Irazuzta S, Appel HM, et al. 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87:S150–62

Fisher RA. 1930. *The Genetical Theory of Natural Selection*. Oxford, UK: Oxford Univ. Press

Fowler CW, Macmahon JA. 1982. Selective extinction and speciation—their influence on the structure and functioning of communities and ecosystems. *Am. Nat.* 119:480–98

Freeland JR, Biss P, Conrad KF, Silvertown J. 2010. Selection pressures have caused genome-wide population differentiation of *Anthoxanthum odoratum* despite the potential for high gene flow. *J. Evol. Biol.* 23:776–82

Fussmann GF, Loreau M, Abrams PA. 2007. Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* 21:465–77

Giraud A, Matic I, Tenaillon O, Clara A, Radman M, et al. 2001. Costs and benefits of high mutation rates: adaptive evolution of bacteria in the mouse gut. *Science* 291:2606–8

Goddard MR, Godfray HCJ, Burt A. 2005. Sex increases the efficacy of natural selection in experimental yeast populations. *Nature* 434:636–40

Gomez P, Buckling A. 2011. Bacteria-phage antagonistic coevolution in soil. *Science* 332:106–9

Goodman AL, Kallstrom G, Faith JJ, Reyes A, Moore A, et al. 2011. Extensive personal human gut microbiota culture collections characterized and manipulated in gnotobiotic mice. *PNAS* 108:6252–57

Gossmann TI, Keightley PD, Eyre-Walker A. 2012. The effect of variation in the effective population size on the rate of adaptive molecular evolution in eukaryotes. *Genome Biol. Evol.* 4:658–67

Gravel D, Bell T, Barbera C, Bouvier T, Pommier T, et al. 2011. Experimental niche evolution alters the strength of the diversity-productivity relationship. *Nature* 469:89–92

Guimarães PR, Jordano P, Thompson JN. 2011. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14:877–85

Haddrill PR, Halligan DL, Tomaras D, Charlesworth B. 2007. Reduced efficacy of selection in regions of the *Drosophila* genome that lack crossing over. *Genome Biol.* 8:R18

Haft RJF, Mittler JE, Traxler B. 2009. Competition favours reduced cost of plasmids to host bacteria. *ISME J.* 3:761–69

Harmon JP, Moran NA, Ives AR. 2009. Species response to environmental change: impacts of food web interactions and evolution. *Science* 323:1347–50

Harrison E, Brockhurst MA. 2012. Plasmid-mediated horizontal gene transfer is a coevolutionary process. *Trends Microbiol.* 20:262–67

Hedrick PW. 2013. Adaptive introgression in animals: examples and comparison to new mutation and standing variation as sources of adaptive variation. *Mol. Ecol.* 22:4606–18

Hekstra DR, Leibler S. 2012. Contingency and statistical laws in replicate microbial closed ecosystems. *Cell* 149:1164–73

Hendry AP, Kinnison MT. 1999. Perspective: The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53:1637–53

Herron MD, Doebeli M. 2013. Parallel evolutionary dynamics of adaptive diversification in *Escherichia coli*. *PLOS Biol.* 11:e1001490

Hongoh Y, Deevong P, Inoue T, Moriya S, Trakulnaleamsai S, et al. 2005. Intra- and interspecific comparisons of bacterial diversity and community structure support coevolution of gut microbiota and termite host. *Appl. Environ. Microbiol.* 71:6590–99

Hughes C, Eastwood R. 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *PNAS* 103:10334–39

Johansson J. 2008. Evolutionary responses to environmental changes: How does competition affect adaptation? *Evolution* 62:421–35

Ketola T, Mikonranta L, Zhang J, Saarinen K, Ormala A-M, et al. 2013. Fluctuating temperature leads to evolution of thermal generalism and preadaptation to novel environments. *Evolution* 67:2936–44

Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain–body size allometry. *Evolution* 33:402–16

Lande R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J. Evol. Biol.* 22:1435–46

Lanfear R, Kokko H, Eyre-Walker A. 2014. Population size and the rate of evolution. *Trends Ecol. Evol.* 29:33–41

Lau JA, Shaw RG, Reich PB, Tiffin P. 2014. Indirect effects drive evolutionary responses to global change. *New Phytol.* 201:335–43

Lavergne S, Mouquet N, Thuiller W, Ronce O. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Evol. Syst.* 41:321–50

Lawrence D, Fiegna F, Behrends V, Bundy JG, Phillimore AB, et al. 2012. Species interactions alter evolutionary responses to a novel environment. *PLOS Biol.* 10:e1001330

Lawrence JG, Ochman H. 1998. Molecular archaeology of the *Escherichia coli* genome. *PNAS* 95:9413–17

Leger EA, Espeland EK. 2010. Coevolution between native and invasive plant competitors: implications for invasive species management. *Evol. Appl.* 3:169–78

Lennon JT, Martiny JBH. 2008. Rapid evolution buffers ecosystem impacts of viruses in a microbial food web. *Ecol. Lett.* 11:1178–88

Levy R, Borenstein E. 2013. Metabolic modeling of species interaction in the human microbiome elucidates community-level assembly rules. *PNAS* 110:12804–9

Lewis HM, Law R. 2007. Effects of dynamics on ecological networks. *J. Theor. Biol.* 247:64–76

Liow LH, Van Valen L, Stenseth NC. 2011. Red Queen: from populations to taxa and communities. *Trends Ecol. Evol.* 26:349–58

Loeuille N. 2010. Influence of evolution on the stability of ecological communities. *Ecol. Lett.* 13:1536–45

Login FH, Balmand S, Vallier A, Vincent-Monegat C, Vigneron A, et al. 2011. Antimicrobial peptides keep insect endosymbionts under control. *Science* 334:362–65

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76

Lynch M. 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. *Am. Nat.* 136:727–41

Lynch M, Gabriel W. 1987. Environmental tolerance. *Am. Nat.* 129:283–303

Mahler DL, Revell LJ, Glor RE, Losos JB. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution* 64:2731–45

Manier MK, Arnold SJ. 2006. Ecological correlates of population genetic structure: a comparative approach using a vertebrate metacommunity. *Proc. R. Soc. B* 273:3001–9

Matthews B, Narwani A, Hausch S, Nonaka E, Peter H, et al. 2011. Toward an integration of evolutionary biology and ecosystem science. *Ecol. Lett.* 14:690–701

Maynard Smith J. 1976. What determines the rate of evolution? *Am. Nat.* 110:331–38

Minot S, Bryson A, Chehoud C, Wu GD, Lewis JD, Bushman DF. 2013. Rapid evolution of the human gut virome. *PNAS* 110:12450–55

Moran NA, Jarvik T. 2010. Lateral transfer of genes from fungi underlies carotenoid production in aphids. *Science* 328:624–27

Munday PL, Warner RR, Monro K, Pandolfi JM, Marshall DJ. 2013. Predicting evolutionary responses to climate change in the sea. *Ecol. Lett.* 16:1488–500

Neher RA, Shraiman BI, Fisher DS. 2010. Rate of adaptation in large sexual populations. *Genetics* 184:467–81

Niklas KJ, Midgley JJ, Rand RH. 2003. Size-dependent species richness: trends within plant communities and across latitude. *Ecol. Lett.* 6:631–36

Nogues-Bravo D. 2009. Predicting the past distribution of species climatic niches. *Glob. Ecol. Biogeogr.* 18:521–31

Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N. 2012. Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Change* 2:747–51

Northfield TD, Ives AR. 2013. Coevolution and the effects of climate change on interacting species. *PLOS Biol.* 11:e1001685

Novozhilov AS, Karev GP, Koonin EV. 2005. Mathematical modeling of evolution of horizontally transferred genes. *Mol. Biol. Evol.* 22:1721–32

Ochman H, Lawrence JG, Groisman EA. 2000. Lateral gene transfer and the nature of bacterial innovation. *Nature* 405:299–304

Ormond CI, Rosenfeld JS, Taylor EB. 2011. Environmental determinants of threespine stickleback species pair evolution and persistence. *Can. J. Fish. Aquat. Sci.* 68:1983–97

Orr HA. 2000. Adaptation and the cost of complexity. *Evolution* 54:13–20

Osmond MM, de Mazancourt C. 2013. How competition affects evolutionary rescue. *Philos. Trans. R. Soc. B* 368:20120085

Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* 325:464–67

Pál C, Papp B, Lercher MJ. 2005. Adaptive evolution of bacterial metabolic networks by horizontal gene transfer. *Nat. Genet.* 37:1372–75

Pantel JH, Leibold MA, Juenger TE. 2011. Population differentiation in *Daphnia* alters community assembly in experimental ponds. *Am. Nat.* 177:314–22

Papadopoulou A, Anastasiou I, Spagopoulou F, Stalimerou M, Terzopoulou S, et al. 2011. Testing the species-genetic diversity correlation in the Aegean archipelago: toward a haplotype-based macroecology? *Am. Nat.* 178:241–55

Perron GG, Lee AEG, Wang Y, Huang WE, Barraclough TG. 2012. Bacterial recombination promotes the evolution of multi-drug-resistance in functionally diverse populations. *Proc. R. Soc. B* 279:1477–84

Peterson AT, Soberon J, Sanchez-Cordero V. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–67

Pfeiffer T, Bonhoeffer S. 2004. Evolution of cross-feeding in microbial populations. *Am. Nat.* 163:E126–35

Post DM, Palkovacs EP. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. B* 364:1629–40

Price TD, Qvarnstrom A, Irwin DE. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. B* 270:1433–40

Schluter D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–74

Schoener TW. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331:426–29

Scoville AG, Pfrender ME. 2010. Phenotypic plasticity facilitates recurrent rapid adaptation to introduced predators. *PNAS* 107:4260–63

Seehausen O, Takimoto G, Roy D, Jokela J. 2008. Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Mol. Ecol.* 17:30–44

Siepielski AM, Benkman CW. 2010. Conflicting selection from an antagonist and a mutualist enhances phenotypic variation in a plant. *Evolution* 64:1120–28

Simpson GG. 1949. *Tempo and Mode in Evolution*. New York: Columbia Univ. Press

Smillie CS, Smith MB, Friedman J, Cordero OX, David LA, Alm EJ. 2011. Ecology drives a global network of gene exchange connecting the human microbiome. *Nature* 480:241–44

Song Y, Endepols S, Klemann N, Richter D, Matuschka FR, et al. 2011. Adaptive introgression of anticoagulant rodent poison resistance by hybridization between old world mice. *Curr. Biol.* 21:1296–301

Stenseth NC, Smith JM. 1984. Coevolution in ecosystems—Red Queen evolution or stasis. *Evolution* 38:870–80

Sunday JM, Bates AE, Dulvy NK. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* 278:1823–30

terHorst CP. 2010. Evolution in response to direct and indirect ecological effects in pitcher plant inquiline communities. *Am. Nat.* 176:675–85

Thomas CM, Nielsen KM. 2005. Mechanisms of, and barriers to, horizontal gene transfer between bacteria. *Nat. Rev. Microbiol.* 3:711–21

Thompson JN. 1999. Specific hypotheses on the geographic mosaic of coevolution. *Am. Nat.* 153:S1–14

Tilman D, Lehman C. 2001. Human-caused environmental change: impacts on plant diversity and evolution. *PNAS* 98:5433–40

Turley NE, Odell WC, Schaefer H, Everwand G, Crawley MJ, Johnson MTJ. 2013. Contemporary evolution of plant growth rate following experimental removal of herbivores. *Am. Nat.* 181(Suppl. 1):S21–34

Urban MC. 2013. Evolution mediates the effects of apex predation on aquatic food webs. *Proc. R. Soc. B* 280:20130859

Van Doorslaer W, Stoks R, Swillen I, Feuchtmayr H, Atkinson D, et al. 2010. Experimental thermal microevolution in community-embedded *Daphnia* populations. *Clim. Res.* 43:81–89

Vellend M, Geber MA. 2005. Connections between species diversity and genetic diversity. *Ecol. Lett.* 8:767–81

Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. B* 275:649–59

Wiedenbeck J, Cohan FM. 2011. Origins of bacterial diversity through horizontal genetic transfer and adaptation to new ecological niches. *FEMS Microbiol. Rev.* 35:957–76

Williams HTP, Lenton TM. 2008. Environmental regulation in a network of simulated microbial ecosystems. *PNAS* 105:10432–37

Yoshida T, Jones LE, Ellner SP, Fussmann GF, Hairston NG. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424:303–6