Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities

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Abstract

Today's scientists are facing the enormous challenge of predicting how climate change will affect species distributions and species assemblages. To do so, ecologists are widely using phenomenological models of species distributions that mainly rely on the concept of species niche and generally ignore species' demography, species' adaptive potential, and biotic interactions. This review examines the potential role of the emerging synthetic discipline of evolutionary community ecology in improving our understanding of how climate change will alter future distribution of biodiversity. We review theoretical and empirical advances about the role of niche evolution, interspecific interactions, and their interplay in altering species geographic ranges and community assembly. We discuss potential ways to integrate complex feedbacks between ecology and evolution in ecological forecasting. We also point at a number of caveats in our understanding of the eco-evolutionary consequences of climate change and highlight several challenges for future research.

INTRODUCTION

Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!

—Charles Darwin

As acknowledged early by Darwin (1859) in his metaphor about old Indian ruins (**Figure 1**), the ecological and evolutionary dynamics of natural systems are fundamentally hard to predict. Although human activities continue to alter Earth's climate and biota at an unprecedented rate, causing changes in species range limits and species extinctions from local to global scale (Parmesan 2006), there is an increasing demand to produce reliable projections of the effects of global changes on biodiversity distribution. The analysis and forecasting of species responses to climate change has been largely influenced by Hutchinson's concept of niche (Colwell & Rangel 2009, citing Hutchinson 1957). Based on this concept, habitat suitability models have been instrumental in the development of predictive biogeography (Elith & Leathwick 2009, Guisan & Thuiller 2005, Thuiller et al. 2008). These models build a multivariate statistical representation of a species niche by relating spatial data of species occurrence or abundance to key environmental variables and then project this niche into the future geographic space according to different scenarios (Guisan & Thuiller 2005). Habitat suitability models have had a compelling importance in predicting general trends of range shifts on large sample of species (for an example on European plants, see Thuiller et al. 2005), which have then been confirmed by empirical trends [for comparable empirical trends, see Hickling et al. (2006) and Lavergne et al. (2006)]. In their simplest form, such models however generally ignore all mechanisms linked to species' demography, species' adaptive potential and interspecific interactions (**Figure 2**), which could seriously limit their use for the development of conservation actions and mitigation measures (Thuiller et al. 2008). As examined later in this
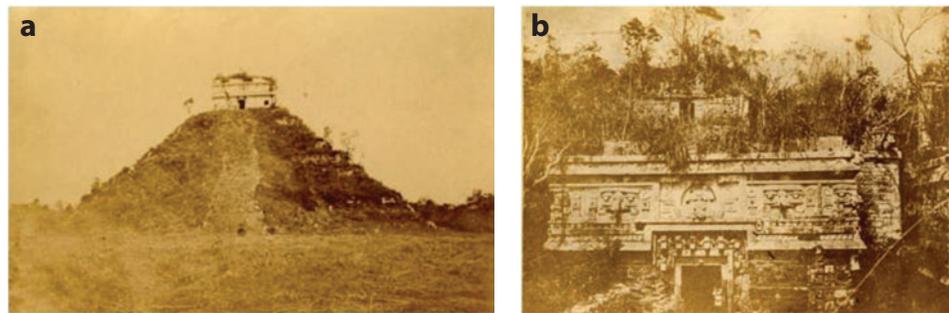

Figure 1

Example of archeological finding that inspired Darwin's metaphor about old Indian ruins being unpredictably invaded by trees. Although it is hard to know which archeological site Darwin might have been referring to, it is likely that he had heard about the numerous rediscoveries of Mayan archeological sites that occurred during the ninteenth century. Here are pictures of tree colonization on ruins of the UNESCO World Heritage site Chichén Itzá (Yucatán, Mexico), taken in 1860 by the French explorer Claude-Joseph Désiré Charnay. (*a*) El Castillo. (*b*) Palacio de Nonnes'. Source: Abbot-Charnay Photograph Collection (1859–1882). Copyright American Philosophical Society.
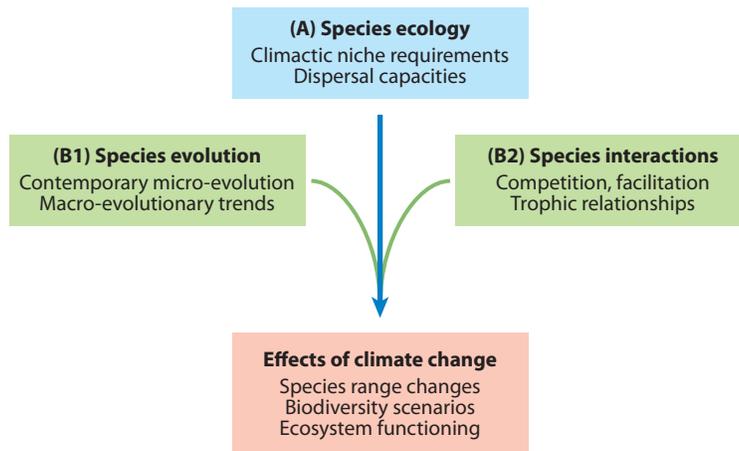
Figure 2

Mechanisms that should be considered in order to adequately project the effect of climate change on species ranges and species assemblages (*red box*). The blue box (*A*) and blue arrow represent the most widely used approaches of species distribution models. The green boxes (*B1* and *B2*) and green arrows represent the mechanisms that have been little envisaged to forecast climate changes effects, so far, namely that species evolve and interact.

review, ongoing developments in the forecasting of species distributions include the so-called process-based models, which integrate several supposedly relevant ecological and evolutionary mechanisms.

We review recent theoretical and empirical advances of the fields of evolutionary ecology and community ecology that may help us to better understand and hopefully forecast the response of species and communities to climate change. We specifically address the following topics:

1. How microevolution within a single species may affect its fundamental niche and its resulting range in constant and changing climates (**Figure 2**, *B1*);
2. How biotic interactions, which set the contour of species' realized niches, may shape future species ranges and communities (**Figure 2**, *B2*);
3. How species evolution and biotic interactions interact together to affect the response of species and communities to climate change; and
4. How to build on such recent developments of evolutionary biology, community ecology, and their emerging synthesis to improve forecasting tools.

We do not aim to develop an exhaustive review of how species geographic ranges and ecological communities are set by niche evolution or interspecific interactions—these topics have been in part reviewed elsewhere (e.g., Leibold & McPeek 2006, Post & Palkovacs 2009, Sexton et al. 2009). The conceptual scope of this review is purposely broad, spanning a number of topics such as micro- and macroevolution of species niches, competition, mutualism or trophic interactions, and ecosystem assembly and functioning. Our goal is to elaborate on the many conceptual links that exist between evolutionary biology and community ecology and show that the emerging synthesis of evolutionary community (and ecosystem) ecology holds much promise for understanding and modeling the biological consequences of climate change.

Fundamental niche: full range of environmental conditions (or niche hypervolume) defined by species' fundamental physiological tolerances

Realized niche: region of the fundamental niche to which the species is restricted due to interspecific interactions, limited dispersal, and historical contingencies

1. HOW EVOLUTION SHAPES SPECIES NICHES AND RANGE DYNAMICS

Ecological forecasting of future species ranges is based on models that generally ignore evolution (but see Kearney et al. 2009). In particular, models have assumed that the statistical or mechanistic relationship between species abundance and environmental characteristics is unchanged at the timescale of the projection. This assumption rests on two related and, until recently, widely accepted conjectures: (*a*) that contemporary evolution has no effect on population dynamics nor geographic ranges, and (*b*) that species niches tend to be phylogenetically conserved.

1.1. Microevolution and Population Dynamics

Ecology and evolution have developed as separate fields based on the distinction between "ecological time" and "evolutionary time" made by Slobodkin (1961). Hairston et al. (2005) have proposed that rapid evolution should be defined as genetic changes occurring fast enough to have a measurable impact on simultaneous ecological change. There is accumulating empirical evidence that evolution can proceed fast (Gingerich 2009, Reznick & Ghalambor 2001) and, more importantly, that the selective process of evolution can significantly affect population dynamics (Hanski & Saccheri 2006, Pelletier et al. 2007; see also reviews by Kokko & López-Sepulcre 2007 and Saccheri & Hanski 2006). This is the case for many introduced species, for which selection-driven phenotypic changes have increased their invasive potential (e.g., Lavergne & Molofsky 2007, Phillips 2009). For instance, local adaptation has occurred over less than 26 generations in the Chinook salmon after its introduction to New Zealand, resulting in a doubling of its vital rates compared to nonlocal genotypes; and this genetic divergence for vital rates far exceeded that predicted on the basis of phenotypic traits thought to be involved in local adaptation (Kinnison et al. 2008). Understanding the consequences of contemporary evolution for the spread or persistence of populations (Kinnison & Hairston 2007, Stockwell et al. 2003) thus requires moving from the simple description of traits divergence toward a more integrative understanding of fitness evolution and its consequences for population dynamics (e.g., Gordon et al. 2009, Kinnison et al. 2008). It also requires quantifying the effect of evolution on phenotypic change and persistence compared to other sources of variation (see Coulson & Tuljapurkar 2008, Ezard et al. 2009, and Ozgul et al. 2009 for diverse attempts of this kind).

Changes in population dynamics can also alter evolutionary trajectories, creating complex eco-evolutionary feedbacks (reviewed in Kinnison & Hairston 2007, Kokko & López-Sepulcre 2007). For instance, fast adaptation to rising temperature occurred in experimental populations of Daphnia subjected to crashes and subsequent growth, but not in more stable populations (Van Doorslaer et al. 2009). The challenges associated with documenting such feedbacks in natural populations—combining information on genetic and phenotypic changes, population dynamics, and selection, as was done, for instance, for selection at the phosphoglucose isomerase (PGI) locus in the Glanville Fritillary butterfly (Hanski & Saccheri 2006, Zheng et al. 2009)—explain the relative rarity of such studies. Still, the increasing number of studies following this approach casts strong doubts on the generality of a clear separation between ecological and evolutionary timescales.

1.2. The Evolutionary Lability of Species Climatic Niches

A common conception is that species niches can reasonably be considered as fixed characteristics on the timescale of climate changes. This assumption has been highly motivated based on the

PHYLOGENETIC NICHE CONSERVATISM

The hypothesis of phylogenetic niche conservatism is an evolutionary conjecture, which stipulates that closely related species should be more ecologically similar than expected based on their timing of phylogenetic divergence (Losos 2008). This hypothesis has usually been tested by measuring a statistical pattern called phylogenetic signal, which is the degree of phylogenetic dependency of a given character (Blomberg & Garland 2002)—a null phylogenetic signal, meaning that this character is totally independent from the phylogeny. As a trait experiencing random evolution (Brownian motion) will inevitably lead to a certain degree of phylogenetic signal, phylogenetic niche conservatism should lead to a stronger phylogenetic signal than expected under Brownian motion. Hence, phylogenetic niche conservatism can also be defined as the tendency for species to exhibit more phylogenetic signal than expected under a scenario of Brownian trait evolution.

hypothesis of niche conservatism (see side bar, Phylogenetic Niche Conservatism), which has been defined as the tendency of a species niche to remain unchanged over time (Pearman et al. 2008, Wiens & Graham 2005). Niche conservatism has been considered paramount to understand allopatric speciation, historical biogeography, patterns of species richness, the spread of introduced species, human history, and the response of species to past and current climate change (Wiens & Graham 2005). The causes of niche conservatism involve the interactions between stabilizing selection, lack of appropriate genetic variation, genetic constraints due to pleiotropy, and gene flow that prevent adaptation to new niches (Holt 1996). More generally, the major evolutionary explanation for niche conservatism lies in the critical difficulty for adaptative traits to evolve in ecological conditions that do not allow population growth (Gomulkiewicz & Houle 2009, Holt 1996).

Genetic variation for climate adaptation, and more generally for traits defining species ecological niches, is pervasive both between and within populations, suggesting a high level of local adaptation to climate at a fine scale (Savolainen et al. 2007) and a high potential to adapt to new climatic conditions (Skelly et al. 2007, Visser 2008). In plants, for instance, regeneration traits (Baskin & Baskin 1998), functional traits linked to phenology, growth or gas exchange (Geber & Griffen 2003), and drought tolerance (Ramirez-Valiente et al. 2009) all exhibit significant genetic variation shaped by selection along environmental gradients. Niche evolutionary lability, however, requires much more than the mere existence of genetic variance for traits involved in niche definition. Information about demographic constraints must be combined with information about genetic constraints to predict which levels of genetic variation are necessary to allow niche expansion (**Figure 3**; Gomulkiewicz & Houle 2009). Thus, joint consideration of genetics and population dynamics will be instrumental to improve our limited understanding of niche evolution or conservatism.

On a macroevolutionary scale, many researchers have observed a certain temporal stasis in species-environment relationships (e.g., Peterson & Nyari 2008, Peterson et al. 1999, Qian & Ricklefs 2004, Ricklefs & Latham 1992, Rodríguez-Sánchez & Arroyo 2008) and concluded it was due to niche conservatism. Recently, the assumption of niche conservatism has been challenged (Losos 2008, Pearman et al. 2008), based on numerous examples of rapid niche shifts during species diversifications (e.g., Evans et al. 2009; for an overview, see Schluter 2000), sometimes on relatively recent timescales (Jakob et al. 2007, Pyron & Burbrink 2009). There is, moreover, evidence for rapid shifts in climatic niches accompanying biological invasions (Beaumont et al. 2009, Broennimann et al. 2007, Medley 2010, Rodder & Lotters 2009, Urban et al. 2007), but the role of evolution in those shifts has yet to be established. Niche conservatism may not be as
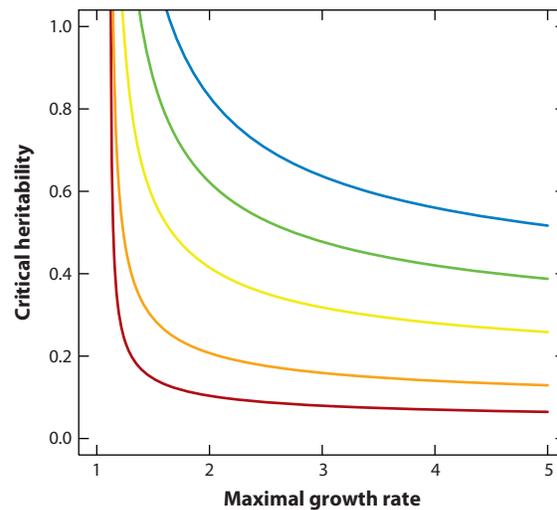
Figure 3

Critical heritability allowing persistence in a changing environment, as a function of demography and rate of environmental change, according to the theoretical predictions derived by Gomulkiewicz & Houle (2009). Their model assumes that the growth rate of the population depends on stabilizing selection on a single phenotypic trait, for which the optimal value is continuously changing at rate k in a directional manner. If the heritability of the character is above some threshold value, the population adapts to the changing environment, and the mean phenotype evolves at rate k with a constant lag behind the moving optimum. If the heritability is below this threshold, the population goes extinct locally. Such critical heritability (Gomulkiewicz and Houle 2009, equation 9) is shown here as a function of the maximal growth rate achieved at the optimal phenotype and for different rates of environmental change (from *red* to *blue*, the optimal phenotype is displaced, respectively, by 0.05, 0.1, 0.2, 0.3 and 0.4 phenotypic standard deviation per generation). Here, the width of the Gaussian fitness function around the optimum is twice the phenotypic standard deviation. Note that the minimal amount of genetic variation allowing adaptation and persistence increases when the maximal growth rate decreases. Adaptation may be impossible whatever the amount of genetic variation when the rate of environmental change is too fast and the population demography not dynamic enough.

widespread as previously assumed, which has potential important consequences for the forecasting of future species ranges.

Furthermore, we argue that focusing solely on the existence of phylogenetic niche conservatism may be of limited interest when studying the consequences of climate change. Previously, a great deal of interest in phylogenetic signal has come from the probable misconception that it measures evolutionary rates. However, a recent simulation-based study compellingly showed that phylogenetic signal and evolutionary rate are not necessarily related (Revell et al. 2008). Many studies that concluded in favor of niche conservatism have not used any specific model of trait evolution and only tested for the existence of a phylogenetic signal in species niches (e.g., Prinzing et al. 2001). Thus, rather than focusing solely on phylogenetic niche conservatism, a more interesting perspective would rather be the inference of rates of niche evolution and their comparison between different groups or clades of interest in order to determine the biological traits that best predict rates of niche evolution. Smith & Beaulieu (2009), for instance, showed significant differences in rates of climatic niche evolution depending on life history in flowering plants. As case studies accumulate, they reveal a large heterogeneity in the rate of niche evolution among groups

of species and among different dimensions of the ecological niche, but clear predictors organizing this heterogeneity remain to be identified.

1.3. The Extent and Limits of Populations' Adaptation to Ongoing Climate Change

Even though observed patterns of species response to climate change are broadly consistent with a pure ecological response, there is evidence that climate change has triggered microevolutionary modifications in many species and populations). Latitudinal clines for genetic markers associated with temperature adaptation in several *Drosophila* species have shifted, allowing these species to keep up with climate warming on three distinct continents (Balanya et al. 2006, Hoffmann & Weeks 2007). The increasing availability of molecular markers and methods to infer molecular signatures of divergent selection allows detecting genetic responses to environmental change in an increasing number of nonmodel species [(reviewed by Hoffmann & Willi (2008) and Reusch & Wood (2007)]. Data on phenotypic evolution in response to climate change remain more scarce and ambiguous (Gienapp et al. 2008), partly because phenotypic plasticity often overwhelms or obscures evolutionary change. Contemporary evolutionary responses to global change involve, in particular, changes in phenology, thermal tolerance, and dispersal traits [reviewed by Gienapp et al. (2008), Parmesan (2006), and Reusch & Wood (2007)].

There is, however, increasing debate about whether microevolution phenomena simply modulate ecological responses to climate change, without constituting real alternatives (Parmesan 2006), or mitigate the negative impacts of future climate change—or, on the contrary, whether they aggravate its consequences (Davis et al. 2005, Jump & Peñuelas 2005). On one hand, a few models suggest that microevolution could mitigate the effects of climate change. Process-based models of tree phenology incorporating the divergence of phenological responses across species ranges predict less severe shifts in species distribution in response to climate change than niche-based models (Morin & Thuiller 2009, Morin et al. 2008). Similarly, the evolution of eggs resistant to desiccation, a trait that shows heritable variation, affects the predicted range shift of Dengue fever mosquitoes in response to climate warming in Australia (Kearney & Porter 2009).

On the other hand, evolutionary response to climate change may be limited by many constraints not incorporated in the previous models. Genetic correlations between traits can strongly impede species adaptive responses to changing climate despite abundant genetic variation (Blows & Hoffmann 2005; see also Etterson & Shaw 2001 for a nice empirical example, or Hellmann & Pineda-Krch 2007). The spatial distribution of genetic variance may also be critical: van Heerwaarden et al. (2009) and Sarup et al. (2009) showed that, in several species of *Drosophila*, low genetic variation for climate-related traits in marginal populations could potentially limit their range expansion. Concern was also expressed about the fact that many microevolution phenomena may be disrupted in the context of current global change, which may compromise the ability of species to respond to climate change as they did in the past (Davis & Shaw 2001). For instance, extinction still occurred at the southern range margins of *Fagus sylvatica*, despite strong signals of genetic adaptation to climate warming (Jump et al. 2006a,b).

Because species are genetically heterogeneous entities, it has been claimed that microevolution has always been involved in ecological responses to climate change, whether these responses correspond to persistence in situ, to shift in distribution, or to extinction (Davis et al. 2005). Understanding how microevolution will affect today's species responses entails shifting our focus from the contemporary evolution of single traits or genes to more integrative multivariate approaches aiming at documenting evolution of fitness and its population dynamics consequences under climate change.

1.4. Toward New Validated Models of Niche Evolution

Several general theoretical models have addressed the coupling of evolutionary responses and population dynamics in the context of a changing environment. A situation of interest is that of a single population confronted by either an abrupt or sustained-and-gradual change in selection pressures causing population decline. Theoretical models have used widely different techniques and assumptions, each with its merits and drawbacks.

Models based on classical quantitative genetics (e.g., Gomulkiewicz & Holt 1995, Gomulkiewicz & Houle 2009, Lynch & Lande 1993) and population genetics (Orr & Unckless 2008) have predicted critical thresholds in the rate of adaptation for population persistence, but neglected complex ecological interactions between individuals in the population. Models of adaptive dynamics have shed a different light on the question of evolutionary rescue by showing that, because of complex ecological interactions, selection does not necessarily favor traits that maximize population density or persistence (Kokko & López-Sepulcre 2007). Complex demography and ecological feedbacks can lead to evolutionary suicide, by which a population evolves trait values that compromise its survival (Ferrière et al. 2004). Classical approaches of adaptive dynamics, however, rest on the assumption of the separation of ecological and evolutionary timescales and focus on describing different types of evolutionary equilibrium, which may not be relevant in the context of ongoing rapid global change. Thus, the main conclusions reached by these models are (*a*) that evolutionary rescue by adaptation in a declining population is difficult, and (*b*) that, counter to common intuition, persistence is not necessarily increased by higher levels of variation for fitness traits. Genetic models must be improved to account for ecological dynamics and adaptive evolution on similar timescales.

Extant models are also in need of empirical validation. Experimental evolution offers a powerful setting to test theoretical predictions about niche evolution. Extinction has, however, been regarded as a nuisance in experimental evolution, and experimental literature demonstrating the conditions under which evolutionary rescue occurs remains scarce (Bell & Collins 2008). Recently, Bell & Gonzalez (2009) demonstrated the increasing probability of adaptive rescue with increasing propagule size in yeast confronted with saline stress, as predicted by theory (Gomulkiewicz & Holt 1995). Antibiotic resistance was also more likely to evolve and rescue a sink population of bacteria from extinction with increasing migration from a nontreated source and with slower rates of change in the selective environment (Perron et al. 2008). Experimental evolution in more natural settings can also be studied through transplantation experiments within and outside the range (Angert 2009, Angert & Schemske 2005, Griffith & Watson 2006).

1.5. Dispersal as a Key Evolutionary Factor

Adaptation and dispersal are often presented as alternative mechanisms whereby a population can respond to changing environmental conditions. Indeed, in the context of a changing environment, dispersal also plays a crucial role in tracking favorable environmental conditions through space (Midgley et al. 2006, Pease et al. 1989, Polechova et al. 2009). Yet, interactions between dispersal and adaptation are more complex than apparent in that simple alternative (Garant et al. 2007). Gene flow, combined with strong demographical asymmetries, in spatially heterogeneous environments is thought to be largely responsible for the slow evolution of the niche in marginal habitats and, thus, a major explanation for niche conservatism and limited species ranges (Bridle & Vines 2007, Holt 2003, Sexton et al. 2009). Theory predicts that dispersal will have complex consequences for the evolution of the niche: It can prevent divergent evolution in marginal populations (Hendry et al. 2001), but it can also help adaptation of small populations through both demographic and genetic

rescue effects (Alleaume-Benharira et al. 2006, Holt 2003, Kawecki 2008). Empirical evidence for the role of gene swamping in limiting species range is yet very elusive (Bridle et al. 2009, Moore & Hendry 2009); rather, it tends to support the idea that dispersal has globally positive effects on fitness in marginal populations (Emery 2009, Kawecki 2008, Tallmon et al. 2004).

Given the extent of local adaptation to climate within species with large geographical ranges, migration of different genotypes could thus have nontrivial consequences for the evolution of range limits (Davis et al. 2005). Dispersal could play different roles in the adaptation and persistence of populations at the trailing and leading edges of a shifting range (Hampe & Petit 2005). Finally, dispersal can also evolve in the context of climate change, with consequences for niche tracking over space (Thomas et al. 2001a) or for metapopulation persistence at regional scales (Massot et al. 2008). Eco-evolutionary forecasting must therefore involve dispersal as a key factor of species responses to climate change, because dispersal will not only directly influence migration rates but also spatial patterns of local adaptation and evolvability, especially at species range margins (Holt 2003).

1.6. Conclusion: The Eco-Evolutionary Forecasting of Species Ranges

A number of questions remain widely open. For all of them, progress seems to depend on our ability to better integrate the genetics of adaptation to climate and population dynamics. In that respect, the historical separation of ecology and evolution has been a strong impediment to our understanding of the consequences of climate change.

First, though species niches, including their fundamental niches, may not be as evolutionarily stable as conventionally assumed, we lack indicators of species attributes (e.g., life-history traits) that could organize the large, empirically observed heterogeneity in niche evolutionary lability. This could then be used to predict the relative rates of adaptations to climate change for large numbers of species or clades.

Second, despite the growing evidence for rapid adaptive evolution in response to climate change, the consequences of evolution on population dynamics and extinction risk remain to be explored. Theoretical models could be useful, in that respect, in predicting when adaptation to new ecological conditions is most likely to occur or not. A greater level of exchange between quantitative genetics theory and adaptive dynamics theory appears timely and appropriate given the need for integrating ecological and evolutionary timescales in population dynamics.

Third, though rapid adaptive evolution at range margins may enhance species range shifts, little is formally understood about the interactions between migration and adaptation in the context of global change. Incorporating the effect of genetic variation both within and between populations into process-based models of species distribution could allow researchers to assess the impact of evolutionary mechanisms in predicted range shifts (e.g., Kearney et al. 2009).

Finally, empirical evidence about eco-evolutionary feedbacks that may affect species responses to climate change lags behind theory (Kokko & López-Sepulcre 2007). There is an urgent need for eco-evolutionary forecasts to be tested and parameterized against experimental data collected in the field. Such data should involve demographic surveys, measurement of selection gradients, and transplant experiments within and outside species ranges. We are clearly in need of more numerous studies in these areas (Sexton et al. 2009).

2. HOW ECOLOGICAL INTERACTIONS SHAPE SPECIES RANGE CHANGES

Species range limits are also highly contingent on biotic interactions that determine species realized niches. If species interactions may not be relevant to predict large-scale, continental-wide species

distributions (e.g., Morin et al. 2007), they may, however, be instrumental to understanding and predicting dynamics of populations and communities at smaller spatial scales. Here we review theory and data that have studying how interspecific interactions, within or between trophic levels, impact local population dynamics and range shifts of particular species.

2.1. Competitive Interactions and Niche Filling Can Modulate Species Ranges

Theoretical models show that, in a stable environment, strong interspecific competition can generate species range limits even in the absence of barriers to dispersal or of environmental gradients [reviewed by Case et al. (2005)]. Along abiotic gradients, interspecific competition can also drive a species range to become narrower or range limits to become sharper than predicted based on species niche requirements only (Case et al. 2005). Since the seminal work of Connell (1961) on barnacles, testing such predictions has been a recurrent theme in experimental ecology [reviewed by Colwell & Fuentes (1975), Connell (1983)]. Recently, this topic has regained much interest in the context of predicting future species distributions and assemblages. Field studies conducted on salamanders, birds, and plants suggest that interspecific competition, usually with closely related species, can indeed limit species geographic ranges (e.g., Baack et al. 2006, Cunningham et al. 2009, Gross & Price 2000).

In a changing environment, spatially explicit simulations further suggest that competition can strongly influence rates of species range shifts and patterns of population extirpation (Brooker et al. 2007, Münkemüller et al. 2009). This happens in particular because, at local scale, competition and niche filling processes can modulate the outcome of species immigration and, thus, prevent species from tracking their climatic niche through space. In plant communities, experiments of seed addition or community invasibility have tested whether recipient communities can resist the immigration of additional species (e.g., Fargione et al. 2003, Klanderud & Totland 2007, Mouquet et al. 2004). These studies suggest that community resistance can be driven by very few species, which are either dominant (Klanderud & Totland 2007) or/and functionally similar to the immigrant species (Fargione et al. 2003). A microcosm experiment with several species of *Drosophila* showed that interspecific interactions can strongly distort species range changes along environmental gradients in response to changing abiotic conditions (Davis et al. 1998a). Observational and experimental studies should now be conducted over large environmental gradients to statistically disentangle the relative effect of competition and abiotic environment on the outcome of species coexistence and species immigration into novel communities, especially in marginal environments occurring on the edge of species ranges.

2.2. Effect of Positive Interactions on Species Ranges and Local Diversity

The effects of positive interactions such as mutualisms or facilitation on species range limits have been less studied theoretically than negative interactions (Case et al. 2005). Species engaged in mutualistic interactions may have difficulty in tracking fast environmental change because of their lower effective colonization rate (Brooker et al. 2007). In plants, for instance, this negative effect should vary with species dependency on pollinators and with the level of potential phenological mismatch between plants and pollinators (Hegland et al. 2009). The influence of mutualistic interactions on species range shifts has been emphasized by studies of invasive species [reviewed by Mitchell et al. (2006)]. Soil mycorrhizal fungi (e.g., Klironomos 2002) or pollinators (Stokes et al. 2006) can produce substantial positive feedbacks on introduced plant populations and enhance their colonization success, at least in the initial phase of invasion. Conversely, population

persistence at the rear edge of species ranges can be limited by pollination limitation on reproductive success, as demonstrated in relict species (e.g., Hampe 2005).

Positive interactions may also influence the structure of entire species assemblages and the maintenance of biodiversity through time (e.g., Molofsky & Bever 2002). For instance, differential phenological shifts can cause mismatches between plant and pollinator populations and lead to the extinctions of plant or pollinator species, with expected consequences on the structure of plant-pollinator networks (e.g., Memmott et al. 2007, Rezende et al. 2007). A recent review concluded that some plant-pollinator systems may be robust against both temporal and spatial mismatches between pairs of species (Hegland et al. 2009); however, repeated losses of generalist species can ultimately cause coextinction cascades in the long term (Memmott et al. 2007).

Facilitation is another type of positive interaction that is pervasive in stressful environments such as alpine ecosystems and enhances biodiversity maintenance at a local scale (e.g., Callaway et al. 2002). Spatially explicit simulations show that facilitation can allow less tolerant species to expand their range beyond that corresponding to their fundamental niche (Brooker et al. 2007, Chen et al. 2009). Global warming could alleviate the harshness of high-elevation ecosystems and, thus decrease, the intensity and number of facilitative interactions. A manipulative study has, however, challenged this simplistic view, showing that earlier snowmelt actually increases positive interactions owing to greater incidence of spring frosts (Wipf et al. 2006). This effect should, however, decrease on a longer term, as spring frosts will become rarer. Thus, if the stabilizing effect of positive interactions (facilitation or pollination) on local species diversity may be quite robust in the short term, continued climate change may ultimately break down positive interactions, causing extinction cascades with a delay effect.

2.3. Trophic Relationships and Species Range Changes

Theoretical models suggest that predation can have diverse effects on the range limits of their prey [reviewed by Case et al. (2005) and Holt & Barfield (2009)]. Sharing a generalist predator with a competitor can result, for instance, in nontrivial patterns of species replacement along environmental gradients due to apparent competition (Holt & Barfield 2009). Although specialist predators are, in general, expected to have a nested distribution within the geographical range of their prey, they can limit the range of their prey when recurrent migration of specialist predators from source populations causes the prey to become extinct in marginal sink populations (Holt & Barfield 2009). Increased herbivory by insects or mollusks in marginal habitats has indeed been shown to restrict the range of several plant species (Bruelheide & Scheidel 1999, Lavergne et al. 2005a). Less intuitively, the presence of predators could potentially expand their prey range when, for instance, increased mortality attenuates the destabilizing effects of competition among prey or when the presence of predators results in higher mobility in the prey (Holt & Barfield 2009).

There is a lack of theoretical studies investigating the consequences of such complex trophic interactions for species range shift with climate change. Food-web interactions can cause compensation in the face of environmental change, such that the loss of some species due to increasing environmental stress releases other species from demographic constraints (Ives & Cardinale 2004). Release from top-down effects can thus cause disproportionate demographic release in prey species. This has been demonstrated experimentally in marine and terrestrial prey-predator or host-parasite systems (Colwell & Fuentes 1975). Many species currently expanding their range, whether exotic or native, are being released from pathogens and herbivores relatively to non-expanding species (Engelkes et al. 2008, Mitchell et al. 2006). Native predators can also slow down the range expansion of introduced species (deRivera et al. 2005, Juliano et al. 2010). In

a microcosm experiment, Davis et al. (1998b) showed that the parasitoid *Leptopilina boulardii* affected ranges, abundance, and coexistence of several *Drosophila* species along artificial temperature gradients. Empirical evidence therefore suggests that natural enemies can control the rates of range shifts of their prey or host species, as well as their final distribution along environmental gradients.

As large herbivores can have pervasive effects on the structure of terrestrial plant communities (Crawley 1983), they may ultimately alter their trajectory under climate change. A recent paleoecological study demonstrates that the collapse of North American megaherbivores altered the structure of plant communities by releasing palatable hardwoods from herbivory pressure, which in turn increased fire regimes in these ecosystems (Gill et al. 2009). An enclosure experiment conducted in an arctic ecosystem showed that large herbivores such as muskoxen and caribou have a major effect on plant community response to simulated warming by buffering their composition change against the strong directional effects of climate warming (Post & Pedersen 2008). Vegetation dynamics as a response to climate change may thus be largely influenced by the occurrence of grazers and their population dynamics.

As species tend to respond to climate change in very individualistic ways (see next section), one of the main impacts of climate change on animal populations will be mediated through the synchrony with their food and habitat resources [reviewed by Parmesan (2006)]. Altered synchrony between prey and predators will generally have negative fitness consequences on predator populations (Visser & Both 2005). This was demonstrated in blue tits populations, where the mismatch between food supply (caterpillars) and nestling demands caused increased energetic costs and reduced fitness of adult birds (Thomas et al. 2001b). The consequences of such mismatching for species range changes are, however, seldom explored (Parmesan 2006). Decoupled trophic interactions due to climate change may compromise population sustainability and, in some cases, affect species range changes (Schweiger et al. 2008). Asynchrony between a butterfly species and its plant hosts due to climate change has caused differential population crashes in the butterfly populations along environmental gradients and ultimately caused the butterfly's range to shift upward and northward (Parmesan 2006). The existence of trophic mismatch in prey-predator and host-parasite systems or the collapse of one partner in the interaction will thus have nontrivial demographic effects and cause complex population and range dynamics, generally depending on the relative environmental niches of species from different trophic levels (Schweiger et al. 2008).

2.4. Nonanalog Versus Stable Species Assemblages

Despite a general trend for species expanding their ranges northward and/or upward or advancing their phenology (Parmesan 2006, Parmesan & Yohe 2003), signature of environmental change on communities seems to be driven by a subset of highly responsive species (Cleland et al. 2006; Lavergne et al. 2005b, 2006; le Roux & McGeoch 2008; Miller-Rushing et al. 2008; Miller-Rushing & Primack 2008, Tingley et al. 2009). This heterogeneity in species responses to climate change will strongly alter the composition of local communities and induce the formation of nonanalog communities, where extant species co-occur in historically unknown combinations (Hobbs et al. 2009, Kullman 2006). A number of extant natural communities may similarly be transient species associations (Collinge & Ray 2009). Fossil records confirm that species assemblages have been much dynamic during periods of climate change and that the emergence of nonanalog communities following climate change is rather the rule than the exception. This pattern has been reported consistently for different biological groups, animals or plants, terrestrial and marine (Jackson & Overpeck 2000, Stewart 2009), which gives large support to a model of individualistic species responses to environmental change (Gleason 1926).

The observations that many ecosystems or communities are being modified into nonanalog species assemblages (Hobbs et al. 2009) raise questions about the outcome of these novel, nonhistorical species interactions. This has stimulated new interest for the inference of community assembly rules (Diamond 1975): Are natural communities mainly assembled through environmental filtering and competitive lotteries (niche-based processes; Chase & Leibold 2003) or through neutral, stochastic processes (Hubbell 2001)? The conclusions of this ongoing debate hold promises for defining simple sets of assembly rules that could be used for forecasting the outcome of new species interactions within communities (for a hierarchical view of these rules, see **Figure 4**). For instance, because competitive interactions and environmental filtering should lead to diverging patterns of community structure in terms of functional traits (e.g., Cornwell & Ackerly 2009) or phylogenetic structure (e.g., Vamosi et al. 2009), empirical signatures of community structure could be used to derive a set of assembly rules to be used in stochastic simulations of future composition of natural communities (**Figure 4b** and **4c**). Alternatively, neutral assembly could prove to be a reasonable assumption for rules of community assembly, rather than niche-based competitive interactions (**Figure 4c**).

Here a continuous trait of potentially high ecological relevance for community assembly rules is depicted by different circle sizes (e.g., specific leaf area in plant communities, beak size in bird communities, etc.). Different steps of community assembly are expected to produce discernable signatures of trait similarity and phylogenetic relatedness within and between communities, which then could be extrapolated to derive stochastic assembly rules for the forecasting of future species assemblages.

A diverging view comes from the observation that some species associations can exhibit relative temporal stability in the fossil record (DiMichele et al. 2004). This may reflect the outcome of strong environmental filters that keep selecting the same species assemblage under a set of given environmental conditions, but may also reflect ecological stabilizing mechanisms that enhance species coexistence (Chesson 2000). Do communities or ecosystems have emergent properties that confer them greater stability or resistance to environmental change? This question has a long tradition in the ecological literature and has received much theoretical treatment (MacArthur 1955, May 1974). At the ecosystem scale, stability in large food webs has been shown to depend on the evolution of stabilizing negative feedbacks and compensation effects (Ackland & Gallagher 2004, Ives & Cardinale 2004). Long-term experiments conducted on grassland have shown that such ecosystems can exhibit striking stability over time, even under simulated warming (Grime et al. 2008), and that much of this temporal stability can be attributed to the stabilizing mechanisms of environmental variability on dominant species with varying life-history strategies (Adler et al. 2006, Thuiller et al. 2007). Much more empirical studies are needed to quantify how these homeostatic effects can be predicted from plant community structure and diversity, and how stabilizing effects can be altered by climate change. So far, no practical framework relating community stability to its structure is reliable enough to draw useful predictions for ecological forecasting.

2.5. Conclusion: Forecasting the Functioning of Future Species Assemblages

Simple microcosm experiments have shown that ignoring species interactions could lead to erroneous predictions about future species ranges based solely on species niche characteristics (Davis et al. 1998b). If the distribution of some species can be well predicted on large spatial scales without accounting for interspecific interactions (Morin et al. 2007), our review suggests that competitive, mutualistic or trophic interactions can also influence the rates at which species are shifting their ranges. Integrating biotic interactions and feedback loops accounting for compensating mechanisms within food webs into forecast models may therefore be critical

Community assembly: ecological and historical processes leading to the construction of ecological communities over time

Environmental filtering: set of environmental factors that an organism must tolerate in order to complete its life cycle, thus driving species with similar adaptations to co-occur together

Neutral assembly: community assembly where individuals of trophically similar species are ecologically equivalent relative to their birth and death rates

Stabilizing mechanisms: mechanisms of negative frequency dependency (rare species tending to have greater vital rates) that allow species coexistence within communities
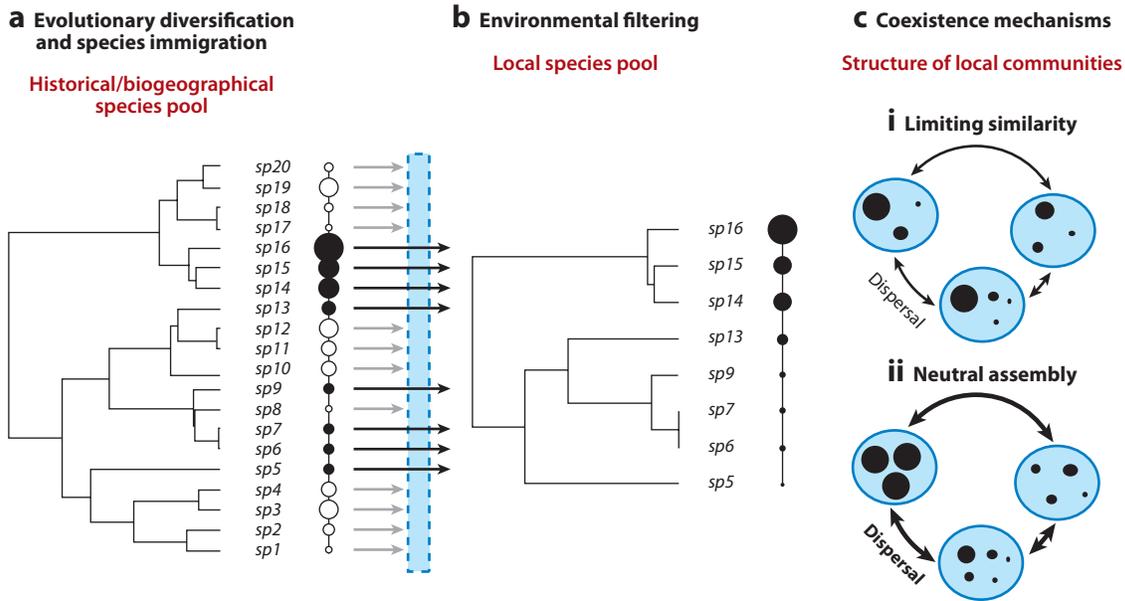
Figure 4

Simulated example showing the ecological and evolutionary mechanisms that can be envisaged to model future species assemblages. Main titles (*a–c*) depict mechanisms, and secondary titles in red depict the levels of biotic organization that are affected at each step. (*a*) The historical species pool of a biogeographic region can emerge through in situ diversification and species immigration, yielding a particular pattern of phylogenetic structure and trait variation along this tree. We simulated species diversification through a random birth-death process, as well as the evolution of two uncorrelated traits (one discrete trait *coded by circle color*, one continuous trait *coded by circle size*) so that they both exhibit a pattern of phylogenetic signal (but phylogenetic signal may not always be the rule; see Section 1.2). (*b*) Local species pools can be constituted through environmental filtering of species according to key physiological tolerances (here represented with *filled circles* versus *open circles*), as easily captured by bioclimatic niche models. Note that environmental filtering may not always be prominent in certain regions. (*c*) More locally, communities occurring in roughly similar environments can be assembled through a set of stochastic rules, including dispersal and two alternative coexistence mechanisms. A first mechanism can be limiting similarity (*i*), which assumes stronger negative interactions (coexistence less likely) between species with similar traits (here with similar *circle sizes*). A second possible assumption is neutral assembly (*ii*), which considers fitness equivalence between all species (coexistence equally likely for any species pairs). Note that under neutral assembly, dispersal is the main structuring mechanism.

to understanding the consequences of climate change on species ranges and assemblages, especially when using small-scale, dynamic, and transient modeling (as opposed to equilibrium models).

Given that species assemblages will certainly not respond as cohesive ensembles to climate forcing, a significant challenge resides in the prediction of how novel interspecific interactions and potential species-resource mismatches will influence species range dynamics and local assemblages. Although the debate over ecosystem assembly rules is still unresolved, it remains unclear whether neutral rules and/or niche-based mechanisms should be incorporated into forecasting models to simulate future species assemblages. Community-level stabilizing processes or simply positive interactions must be taken into account in order to predict the future of local assemblages, as the breakdown of such processes may cause delayed, unprecedented extinction cascades. The delayed effect of breakdowns in mechanisms allowing local maintenance of biodiversity has not been accounted for in predictive modeling so far.

3. THE INTERPLAY BETWEEN SPECIES EVOLUTION AND ECOLOGICAL INTERACTIONS

Both species evolution and biotic interactions can be instrumental to understanding how species ranges and communities will be set in the future. However, there is also growing evidence for eco-evolutionary feedbacks within ecosystems, that is, reciprocal feedbacks between community interactions and evolutionary processes (Haloin & Strauss 2008, Post & Palkovacs 2009). Here we review how community functioning and species evolution are potentially linked in a number of ways and how this may influence the consequences of global changes.

3.1. Microevolution Affects Ecosystem Assembly and Functioning

A number of theoretical and empirical studies have focused on the consequences of genetic variation on community and ecosystem functioning [reviewed by Hughes et al. (2008a)]. This field of research is encapsulated under the name of community or ecosystem genetics (Whitham et al. 2006). Most studies focus on dominant or keystone species, because they have potentially important cascading effects throughout ecosystems. Genetic composition of populations, that is, genotype identity but also genetic diversity, was thus shown to influence the community structure of natural enemies and competitors and a number of ecosystem processes (Bailey et al. 2009, Hughes et al. 2008a, Vellend & Geber 2005, Whitham et al. 2006). In plants, for instance, genetic variation in root allelopathic or leaf secondary compounds can have pervasive effects on the composition and diversity of plant and arthropod communities (e.g., Bangert et al. 2006, Crutsinger et al. 2006, Johnson et al. 2006, Lankau & Strauss 2007). Genetic diversity may have an effect per se, creating spatially variable selective pressure for competitors or natural enemies, or because it allows evolutionary change of species traits that in turn alter the outcome of biotic interactions. For instance, models suggest that the stability of large food webs is enhanced by adaptive evolution (Ackland & Gallagher 2004, Kondoh 2003). Microcosm experiments showed that the evolution of prey resistance to predators indeed influenced predator-prey population cycles (Jones et al. 2009, Yoshida et al. 2003).

As species diversity might act as insurance against environmental changes (Loreau et al. 2003, Yachi & Loreau 1999), genetic diversity should also have the potential to protect communities from environmental variability. Recent microcosm experiments with bacteria showed that genetic variation allows community resistance to environmental stress (Boles et al. 2005). Booth & Grime (2003) showed that grassland communities tend to retain greater species diversity over time when intraspecific genetic diversity is increased. This pattern is due to complex genotype-to-genotype interactions that promote species coexistence (Lankau 2009, Whitlock et al. 2007). Genotypic diversity of the eelgrass, *Zostera marina* L., was shown to positively affect seagrass ecosystem functioning against global warning (Ehlers et al. 2008), enhancing ecosystem recovery (biomass production, faunal abundance) after large perturbations caused by climatic extremes or massive herbivory (Hughes & Stachowicz 2004, Reusch et al. 2005).

Similar experiments have yet to be conducted with more complex ecological systems to better evaluate the effect of genetic diversity and species evolution on ecosystem functioning and stability, especially in nonequilibrium conditions caused by strong climate forcing. Although field studies support the prediction that species evolution affects community structure and functioning (Bailey et al. 2009, Lankau 2009, Lankau & Strauss 2007, Palkovacs et al. 2009), such studies have been limited to very few ecological theatres. Whether genetic effects on community and ecosystems are widespread is still an open question.

3.2. Community Context Affects Evolutionary Trajectories

Theoretical models show that the community context, especially the patterns of niche occupancy, can strongly alter the fate of adaptive evolution and range dynamics (de Mazancourt et al. 2008, Johansson 2008, Price & Kirkpatrick 2009). Character displacement due to competition for resources or reproductive interference has long been documented both theoretically and empirically (Goldberg & Lande 2006). More recently, the evolution of character displacement has been connected more closely to the response of species to environmental change or to the definition of range limits. Interspecific competition appears to be a potent constraint limiting the evolutionary expansion of the ecological niche: Evolutionary models including the effect of competition for resources predict more readily the evolution of narrow range limits (Case & Taper 2000, Goldberg & Lande 2007) than single-species models of range evolution (Kirkpatrick & Barton 1997). Evolutionary constraints set by interspecific competition also represent an interesting theoretical alternative to the disruptive effect of gene flow at range margins, for which there is limited evidence (Price & Kirkpatrick 2009). In Galapagos medium ground finches, evolutionary changes in body size after different drought events differed drastically depending on the community context: In the absence of large competitors, larger body size evolved to exploit larger seeds after the drought, whereas smaller size evolved in the same circumstance but in the presence of large ground finches (Grant & Grant 2006). This supports the idea that competition could modify the species evolutionary response to climate change. Several theoretical studies suggest that species diversity in a community could severely inhibit evolutionary responses to environmental changes within species (de Mazancourt et al. 2008, Johansson 2008). To our knowledge, this idea has not yet been tested empirically. There is comparatively little theoretical understanding of how trophic interactions or positive interactions may set limits on the evolution of species range [but see Nuismer & Kirkpatrick (2003) for a model of host-parasite coevolution] despite the ecological importance of such interactions and the empirical evidence for coevolution in many ecological systems.

As reviewed above, the fossil record shows continuous reshuffling of species assemblages over time (Stewart 2009). Although environmental filtering may promote stabilizing selection (Ackerly 2003), continuous biotic exchanges between regions or continents likely promotes evolutionary change. As different community members continuously exert selective pressures on each other, changes in community composition are potentially of strong evolutionary significance (Johnson & Stinchcombe 2007, Stewart 2009). This view is supported by studies of contemporary invasions, where native communities have adapted following the immigration of an alien species that had a short or inexistent history of coexistence with native species [reviewed by Strauss et al. (2006) and Vellend et al. (2007)]. Shifts to an exotic host or prey have caused disruptive selection in favor of various traits between populations of native parasites or predators (Carroll et al. 2001, Filchak et al. 2000, Phillips & Shine 2004). Alternatively, some native species have increased their resistance to alien herbivores or predators (Palkovacs et al. 2009, Trussell & Smith 2000, Vourc'h et al. 2001). Some native fish or plant species have also successfully adapted against novel competitors (Callaway et al. 2005, Robinson & Parsons 2002).

Thus, species adaptive responses may affect the fate of novel species immigration into previously established communities. Natural communities can thus be viewed as a mosaic of coevolutionary trajectories within and between trophic levels (Thompson 2005), which may render the dynamics of ecosystems quite unpredictable. Focusing on predicting evolutionary change in keystone, dominant species may, however, help in organizing this complexity, if such species are drivers of ecosystem dynamics together with climate forcing.

3.3. Can Knowing Species Evolutionary History Help to Predict Future Ecosystem Structure?

An emerging field of investigation could potentially prove to be useful in developing new forecasting tools. This is the field of community (and ecosystem) phylogenetics, which aims to determine how evolutionary history of species pools—that is, their phylogenetic relationships—influences the processes of species assembly and biotic interactions (Cavender-Bares et al. 2009, Webb et al. 2002). This new field makes an interesting link between diversification processes (speciation and niche and traits evolution) and the ecological processes that drive species to co-occur together or feed on each other. At the scale of communities, it has been demonstrated that species are generally not randomly distributed within communities and along environmental gradients with respect to their phylogenetic relationships (Cavender-Bares et al. 2009, Emerson & Gillespie 2008, Johnson & Stinchcombe 2007) (see side bar, Community Phylogenetic Structure). At the scale of ecosystems, there is also much evidence that networks of trophic and mutualistic interactions are phylogenetically structured [reviewed by Thuiller et al. (2010b)]. For example, Gilbert & Webb (2007) showed that shifts of pathogens between tropical tree species decrease with phylogenetic distance between tree species.

Thanks to these seemingly simple conclusions, the field of community phylogenetics holds great promise toward unraveling general assembly rules of species assemblages (**Figure 4**)—rules that then could be used in ecological forecasting, although such an extrapolation has not been made yet. Empirical validation of these rules is made possible by studying species introductions, and testing whether naturalization of immigrant species depends on their phylogenetic relatedness to local communities (the so-called Darwin's naturalization conundrum; Darwin 1859). The few empirical tests of this hypothesis tend to confirm the general expectation that naturalization of introduced species is generally enhanced by their phylogenetic relatedness with the local flora at larger spatial scales. This may be because environment filters for broad adaptations and closely related species may tend to have more similar niches than two species taken at random (Thuiller et al. 2010b), however, the latter argument may not always be true (see Section 1.2). This effect is, however, reversed at the local scale, where competition for resources or natural enemies should prevent introduced species that are phylogenetically related to native communtiies from establishing and spreading (Thuiller et al. 2010b). Such patterns have been replicated using a small-scale bacterial microcosm experiment (Jiang et al. 2010). This field is largely plant oriented so more empirical data are clearly needed especially on animal taxa. What emerges from recent reviews is that

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COMMUNITY PHYLOGENETIC STRUCTURE

As reviewed by Vamosi et al. (2009), two patterns of community phylogenetic structure are commonly found: (*a*) phylogenetic clustering within communities, as a result of strong environmental filtering on phylogenetically conserved traits (e.g., Kembel & Hubbell 2006), and (*b*) phylogenetic overdispersion, often due to competitive exclusion of closely related species sharing similar niches (e.g., Lovette & Hochachka 2006). Although nonrandom phylogenetic structure tends to rule out neutral assembly of communities, it is however challenging to distinguish between different niche-based scenarios that may operate at different spatial, temporal, and phylogenetic scales (Cavender-Bares et al. 2009). One interesting approach is to compare observed phylogenetic patterns to simulated ones (Kembel 2009, Kraft et al. 2007) and study community assembly from both a phylogenetic and a functional trait viewpoint in the same analytical approach (e.g., Prinzing et al. 2008).

naturalization of an immigrant species may result from various ecological mechanisms of biotic resistance that are not necessarily revealed by species phylogeny alone (Thuiller et al. 2010b). It thus seems that the combination of traits and phylogenetic information (which all together can potentially capture much niche variation) would be more useful in deriving assembly rules to predict the outcome of species sorting along environmental gradients and, later, species assembly within local communities (**Figure 4**).

3.4. Conclusion: Can We Forecast the Eco-Evolutionary Dynamics of Communities?

In some systems, evolutionary change is a critical determinant of ecological dynamics and strongly interacts with ecosystem processes to create eco-evolutionary feedback loops within ecosystems (Carroll et al. 2007, Fussmann et al. 2007, Post & Palkovacs 2009). As highlighted above, coupled evolutionary and ecosystem dynamics have been used to examine only microcosm ecological systems with short generations times and simple genetic structures such as clonal structure (e.g., Jones et al. 2009). Although field evidence suggests that some eco-evolutionary feedbacks may be operating, for instance, in terrestrial plant or stream communities (reviewed above), it is still unclear how pervasive these feedbacks are in nature and whether integrating these feedbacks into predictive models will actually improve them.

For terrestrial plant communities, expected changes in functional traits with important ecosystem consequences (Whitham et al. 2006), driven by climatic or biotic selective pressure, could be used to better depict the spatially variable effects of keystone species on communities and ecosystems. In addition, the evolutionary legacy depicted by the phylogenetic structure of communities and ecosystems has the potential to highlight major assembly rules of species assemblages. If some rules prove to be pervasive at certain spatial scales, they could be used to predict future community composition (through relative effects of neutral and niche-based dynamics) or networks of trophic or mutualistic relationships (through a probabilistic prediction of host-prey shifts, for example).

4. ANOTHER LOOK AT DARWIN'S OLD INDIAN RUINS

With his metaphor about old Indian ruins, Darwin emphasized the unpredictable nature of ecological and evolutionary dynamics of species and communities. Since then, much progress has been made toward understanding how evolution and biotic interactions shape species geographic ranges and composition of natural communities, as well as how they interplay with each other to drive biodiversity responses into environmental changes. Here we discuss strategies to integrate these advances into a modeling framework from a forecasting perspective. Finally, we examine the contribution of the emerging synthesis between evolutionary biology and community ecology, for climate change modeling in particular and for understanding the dynamics of ecological systems in general.

4.1. A Look Back at Current Species Distribution Models

Phenomenological habitat suitability models, which statistically relate species' occurrence or abundance to key environmental variables, have been the tool of choice to project the effects of climate and land use changes on species distributions and species assemblages (Elith & Leathwick 2009, Guisan & Thuiller 2005, Thuiller et al. 2008). Most habitat suitability models ignore mechanisms driving species evolution, species' demography, and species' interactions. They actually assume that the fitted relationship between species' occurrence or abundance of a given species and the

environmental conditions measured at a site is a good surrogate for such demographic processes (Austin 2007, Thuiller et al. 2010a).

Alternatively, process-based models of species distribution that usually rely on the understanding and modeling of key demographic processes (growth, birth, death, dispersal) are supposed to be more appropriate and robust (Jeltsch et al. 2008, Thuiller et al. 2008). However, few of them have been applied to large numbers of species because they usually require long-term time series data and detailed knowledge of the species of interest (Thuiller et al. 2008). The most well-known and widely applied process-based models of species distribution in a climate change context are the so-called forest gap models (Bugmann 2001). Latest developments include relatively simple biotic interaction rules and moderately complex dispersal models (Lischke et al. 2006). Species-specific mechanistic niche models have been recently developed and are considered very promising tools because they aim at capturing the fundamental niche of species (Kearney & Porter 2009). However, despite a few particular exceptions of studies on well-documented species, very few of the above-mentioned models include simultaneously biotic interactions, dispersal, and the potential for rapid adaptation, and they do not include any community assembly rule.

4.2. Developing an Eco-Evolutionary Approach to Biodiversity Forecasting

Incorporating eco-evolutionary feedbacks into applied mechanistic models is obviously a serious research challenge. As reviewed above, it would ideally require combining information on genetic changes and fitness consequences, population dynamics, and selective pressures on populations along environmental gradients to account for the importance of evolutionary effects on species range changes under climate change. Applied mechanistic models are developed with the aim of providing quantitative and detailed projections of species range change in a climate change context and then striving to incorporate more ecological details. Recent developments have, for instance, tried to incorporate local or rapid adaptation into spatially explicit models of species distribution (Kearney & Porter 2009, Kuparinen & Schurr 2007). The modeling framework AMELIE (Kuparinen & Schurr 2007) links the spatio-temporal dynamics of plant populations and genotypes; is flexible in its description of life histories, seed and pollen dispersal, and reproductive systems; and accounts for demographic and environmental stochasticity. The AMELIE framework could thus be used for incorporating evolutionary processes into distribution modeling, given that sufficient demographic and genetic data are available or given that reasonable assumptions on parameter ranges can be made. The effects of biotic interactions are nevertheless not accounted for in the AMELIE framework. Similar developments have been made for modeling the range expansion of animals in a climate change context (Kearney & Porter 2009, Kearney et al. 2009). The use of general models of energy and mass transfer for animals—combining information on the behavior, physiology, and morphology of an organism with environmental data to predict the climatic component of an organism's fundamental niche—are really promising (Kearney et al. 2009). Because these models are trait based, as opposed to distribution based, they also provide the opportunity to explicitly assess the impact of plastic or evolutionary changes in key limiting traits (Kramer et al. 2010, Morin et al. 2007). Then, integrating community assembly rules to account for the effects of community structure into the dynamics of species range change constitutes an exciting next step.

Species distribution models explicitly accounting for biotic interactions are now numerous but mostly developed for plants. Forest gap models, landscape models, dynamic vegetation models, or hierarchical population models include biotic interactions at the same trophic level often modeled as competition for light [reviewed by Thuiller et al. (2008)]. Thus, one can imagine feeding such models with parameter values or ranges depicting assembly rules that would have been determined

earlier from studies of community assembly (briefly reviewed above). However, despite a few examples, models explicitly accounting for multitrophic interactions remain scarce (e.g., Anderson et al. 2009, Hughes et al. 2008b).

Forecasting models should be fed with and tested against empirical data. Longterm time-series data, traits variability across populations and along environmental gradients, and genetic diversity and population dynamics are necessary information for a clear integration of eco-evolutionary information into species distribution models. Not surprisingly, the most innovative frameworks include mechanistic modeling of the niche; that is, biotic interactions or rapid adaptations have been developed for well-studied organisms, mostly invasive species, pests, or species of economic value (Kearney & Porter 2009, Kearney et al. 2009).

4.3. The Necessary Synthesis Between Evolutionary Biology and Ecosystem Ecology

Over the past few years, the study of eco-evolutionary dynamics of communities and ecosystems has been emerging as a synthetic discipline, integrating many concepts of both evolutionary biology and community ecology (Fussmann et al. 2007, Johnson & Stinchcombe 2007). By drawing explicit links between species evolution, species assemblages, and ecosystem functioning, this emerging field, often termed evolutionary community ecology, may fundamentally change our understanding of the evolutionary and ecological responses of species and communities to climate change. We have reviewed a number of theoretical and empirical advances regarding the role of niche evolution, interspecific interactions, and their interplay in altering species geographic ranges and community assembly (summarized below). There are potential ways to integrate these mechanisms into ecological forecasting, but a number of questions remain open and will pose important challenges for the development of new forecasting tools (listed below). Maybe more importantly, thanks to this emerging eco-evolutionary synthesis, the long-lasting separation between evolutionary and ecosystem studies is now ending. There is compelling evidence that complex feedbacks at the scale of communities and entire ecosystems set the scene for the evolutionary play, and that evolutionary change may not only influence ecological dynamics of populations and communities, but also ecosystem processes (Fussmann et al. 2007, Haloin & Strauss 2008, Post & Palkovacs 2009). The study of eco-evolutionary dynamics of species, communities, and ecosystems should ultimately provide an integrated view of the spatial and temporal dynamics of different biodiversity components and how these components respond to human-driven environmental changes.

SUMMARY POINTS

1. Species niches are constantly shaped by natural selection, and niche conservatism may not be as widespread as previously assumed.

2. There is growing evidence for rapid adaptive evolution in response to climate change. But the consequences of this for population dynamics and species range shifts remain quite unexplored.

3. Ecological interactions such as competition, positive interactions, and trophic relationships can control population dynamics along environmental gradients and affect rates of species range shifts.

4. Species assemblages are not responding cohesively to climate change. Rather, species respond individualistically, making the assembly of future communities challenging to model and predict.

5. Species microevolution and community dynamics are potentially linked by feedbacks. Changes in dominant species genetic structure can affect the community or ecosystem functioning; and in turn, change in community context influences species evolution.

6. Communities and ecosystems are not randomly structured with respect to species evolutionary origins, and observed patterns of phylogenetic structure can reveal key assembly processes.

7. Modeling tools are currently under development to integrate evolution and species interactions into species distribution models.

FUTURE ISSUES

1. We need biological indicators (e.g., species traits) that can organize the large empirically observed heterogeneity in niche evolutionary lability and can be used as predictors of rates of niche evolution for large numbers of species or clades.

2. A tighter integration between population demography and genetics must be achieved from both a theoretical and an empirical point of view to address issues related to the effects of climate change on species range and persistence.

3. Genetic models must be improved to account for ecological dynamics and adaptive evolution on similar timescales.

4. Eco-evolutionary forecasting must involve dispersal as a key factor of species evolution, geographic range, and response to global change.

5. More progress must be made to determine the relative importance of neutral versus niche-based rules of ecosystem assembly, so that they can be used to simulate future species assemblages.

6. The prevalence of extended genetic effects on communities and ecosystems is not well understood, and more studies are needed to experimentally demonstrate the coupling of species evolution and ecosystem functioning in natural conditions.

7. Species responses to current climate change will likely point to eco-evolutionary dynamics, and there is urgent need for testing and parameterization of eco-evolutionary forecasts against experimental data collected in the field.

DISCLOSURE STATEMENT

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LITERATURE CITED

Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.* 164:S165–84

Ackland GJ, Gallagher ID. 2004. Stabilization of large generalized Lotka-Volterra foodwebs by evolutionary feedback. *Phys. Rev. Lett.* 93:158701.1–4

Adler PB, HilleRisLambers J, Kyriakidis PC, Guan QF, Levine JM. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl. Acad. Sci. USA* 103:12793–98

Alleaume-Benharira M, Pen IR, Ronce O. 2006. Geographical patterns of adaptation within a species' range: interactions between drift and gene flow. *J. Evol. Biol.* 19:203–15

Anderson BJ, Akcakaya HR, Araujo MB, Fordham DA, Martinez-Meyer E, et al. 2009. Dynamics of range margins for metapopulations under climate change. *Proc. R. Soc. Lond. B* 276:1415–20

Angert AL. 2009. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proc. Natl. Acad. Sci. USA* 106:19693–98

Angert AL, Schemske DW. 2005. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution* 59:1671–84

Austin M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* 200:1–19

Baack EJ, Emery NC, Stanton ML. 2006. Ecological factors limiting the distribution of Gilia tricolor in a California grassland mosaic. *Ecology* 87:2736–45

Bailey JK, Schweitzer JA, Ubeda F, Koricheva J, LeRoy CJ, et al. 2009. From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philos. Trans. R. Soc. B* 364:1607–16

Balanya J, Oller JM, Huey RB, Gilchrist GW, Serra L. 2006. Global genetic change tracks global climate warming in *Drosophila* subobscura. *Science* 313:1773–75

Bangert RK, Turek RJ, Rehill BJ, Wimp GM, Schweitzer JA, et al. 2006. A genetic similarity rule determines arthropod community structure. *Mol. Ecol.* 15:1379–91

Baskin CC, Baskin JM. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. San Diego, CA: Academic. 666 pp.

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers. Distrib.* 15:409–20

Bell G, Collins S. 2008. Adaptation, extinction and global change. *Evol. Appl.* 1:3–16

Bell G, Gonzalez A. 2009. Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* 12:942–48

Blomberg SP, Garland TJ. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.* 15:899–910

Blows MW, Hoffmann AA. 2005. A reassessment of genetic limits to evolutionary change. *Ecology* 86:1371–84

Boles BR, Thoendel M, Singh PK. 2005. Genetic variation in biofilms and the insurance effects of diversity. *Microbiology* 151:2816–18

Booth RE, Grime JP. 2003. Effects of genetic impoverishment on plant community diversity. *J. Ecol.* 91:721–30

Bridle JR, Gavaz S, Kennington WJ. 2009. Testing limits to adaptation along altitudinal gradients in rainforest *Drosophila*. *Proc. R. Soc. Lond. B* 276:1507–15

Bridle JR, Vines TH. 2007. Limits to evolution at range margins: When and why does adaptation fail? *Trends Ecol. Evol.* 22:140–47

Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A. 2007. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* 10:701–9

Brooker RW, Travis JMJ, Clark EJ, Dytham C. 2007. Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *J. Theor. Biol.* 245:59–65

Bruelheide H, Scheidel U. 1999. Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *J. Ecol.* 87:839–48

Bugmann H. 2001. A review of forest gap models. *Clim. Change* 51:259–305

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–48

Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM. 2005. Natural selection for resistance to the allelopathic effects of invasive plants. *J. Ecol.* 93:576–83

Carroll SP, Dingle H, Famula TR, Fox CW. 2001. Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. *Genetica* 112:257–72

Carroll SP, Hendry AP, Reznick DN, Fox CW. 2007. Evolution on ecological time-scales. *Funct. Ecol.* 21:387–93

Case TJ, Holt RD, McPeek MA, Keitt TH. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108:28–46

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

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12:693–715

Chase JM, Leibold MA. 2003. *Ecological Niches*. Chicago: Chicago Univ. Press

Chen SY, Xu J, Maestre FT, Chu CJ, Wang G, Xiao S. 2009. Beyond dual-lattice models: incorporating plant strategies when modeling the interplay between facilitation and competition along environmental severity gradients. *J. Theor. Biol.* 258:266–73

Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31:343–66

Cleland EE, Chiariello NR, Loarie SR, Mooney HA, Field CB. 2006. Diverse responses of phenology to global changes in a grassland ecosystem. *Proc. Natl. Acad. Sci. USA* 103:13740–44

Collinge SK, Ray C. 2009. Transient patterns in the assembly of vernal pool plant communities. *Ecology* 90:3313–23

Colwell RK, Fuentes ER. 1975. Experimental studies of the niche. *Annu. Rev. Ecol. Syst.* 6:281–310

Colwell RK, Rangel TF. 2009. Hutchinson's duality: the once and future niche. *Proc. Natl. Acad. Sci. USA* 106:19651–58

Connell JH. 1961. Influence of interspecific competition and other factors on distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–23

Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661–96

Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.* 79:109–26

Coulson T, Tuljapurkar S. 2008. The dynamics of a quantitative trait in an age-structured population living in a variable environment. *Am. Nat.* 172:599–612

Crawley MJ. 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. Oxford: Blackwell Sci.

Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313:966–68

Cunningham HR, Rissler LJ, Apodaca JJ. 2009. Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. *J. Anim. Ecol.* 78:52–62

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S. 1998a. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–86

Davis AJ, Lawton JH, Shorrocks B, Jenkinson LS. 1998b. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *J. Anim. Ecol.* 67:600–12

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292:673–79

Davis MB, Shaw RG, Etterson JR. 2005. Evolutionary responses to changing climate. *Ecology* 86:1704–14

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

deRivera CE, Ruiz GM, Hines AH, Jivoff P. 2005. Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology* 86:3364–76

Diamond JM. 1975. Assembly of species communities. In *Ecology and Evolution of Communities*, ed. ML Cody, JM Diamond, pp. 342–444. Cambridge, MA: Harvard Univ. Press

DiMichele WA, Behrensmeyer AK, Olszewski TD, Labandeira CC, Pandolfi JM, et al. 2004. Long-term stasis in ecological assemblages: Evidence from the fossil record. *Annu. Rev. Ecol. Evol. Syst.* 35:285–322

Ehlers A, Worm B, Reusch TBH. 2008. Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Mar. Ecol. Prog. Ser.* 355:1–7

Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40:677–97

Emerson BC, Gillespie RG. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol. Evol.* 23:619–30

Emery NC. 2009. Ecological limits and fitness consequences of cross-gradient pollen movement in *Lasthenia fremontii*. *Am. Nat.* 174:221–35

Engelkes T, Morrien E, Verhoeven KJF, Bezemer TM, Biere A, et al. 2008. Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* 456:946–48

Etterson JR, Shaw RG. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294:151–54

Evans MEK, Smith SA, Flynn RS, Donoghue MJ. 2009. Climate, niche evolution, and diversification of the "bird-cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *Am. Nat.* 173:225–40

Ezard THG, Cote SD, Pelletier F. 2009. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philos. Trans. R. Soc. B* 364:1491–98

Fargione J, Brown CS, Tilman D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. USA* 100:8916–20

Ferrière R, Dieckmann U, Couvet D, eds. 2004. *Evolutionary Conservation Biology*. Cambridge, UK: Cambridge Univ. Press

Filchak KE, Roethele JB, Feder JL. 2000. Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* 407:739–42

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

Garant D, Forde SE, Hendry AP. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct. Ecol.* 21:434–43

Geber MA, Griffen LR. 2003. Inheritance and natural selection on functional traits. *Int. J. Plant Sci.* 164:S21–42

Gienapp P, Teplitsky C, Alho JS, Mills JA, Merila J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* 17:167–78

Gilbert GS, Webb CO. 2007. Phylogenetic signal in plant pathogen–host range. *Proc. Natl. Acad. Sci. USA* 104:4979–83

Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326:1100–3

Gingerich PD. 2009. Rates of evolution. *Annu. Rev. Ecol. Evol. Syst.* 40:657–75

Reviews the field of community phylogenetics, with an emphasis on insular environments.

Provides a milestone conceptual review about the emerging field of evolutionary community ecology.

Gleason HA. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53:7–26

Goldberg EE, Lande R. 2006. Ecological and reproductive character displacement on an environmental gradient. *Evolution* 60:1344–57

Goldberg EE, Lande R. 2007. Species' borders and dispersal barriers. *Am. Nat.* 170:297–304

Gomulkiewicz R, Holt RD. 1995. When does evolution by natural-selection prevent extinction. *Evolution* 49:201–7

Gomulkiewicz R, Houle D. 2009. Demographic and genetic constraints on evolution. *Am. Nat.* 174:E218–29

Gordon SP, Reznick DN, Kinnison MT, Bryant MJ, Weese DJ, et al. 2009. Adaptive changes in life history and survival following a New Guppy Introduction. *Am. Nat.* 174:34–45

Grant PR, Grant BR. 2006. Evolution of character displacement in Darwin's finches. *Science* 313:224–26

Griffith TM, Watson MA. 2006. Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *Am. Nat.* 167:153–64

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proc. Natl. Acad. Sci. USA* 105:10028–32

Gross SJ, Price TD. 2000. Determinants of the northern and southern range limits of a warbler. *J. Biogeogr.* 27:869–78

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8:993–1009

Hairston NH, Ellner SP, Geber MA, Yoshida T, Fox JA. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8:1114–27

Haloin JR, Strauss SY. 2008. Interplay between ecological communities and evolution review of feedbacks from microevolutionary to macroevolutionary scales. *Ann. NY Acad. Sci.* 2008:87–125

Hampe A. 2005. Fecundity limits in *Frangula alnus* (Rhamnaceae) relict populations at the species' southern range margin. *Oecologia* 143:377–86

Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8:461–67

Hanski I, Saccheri I. 2006. Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biol.* 4:719–26

Hegland SJ, Nielsen A, Lazaro A, Bjerknes AL, Totland O. 2009. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* 12:184–95

Hellmann JJ, Pineda-Krch M. 2007. Constraints and reinforcement on adaptation under climate change: selection of genetically correlated traits. *Biol. Conserv.* 137:599–609

Hendry AP, Day T, Taylor EB. 2001. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* 55:459–66

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.* 12:450–55

Hobbs RJ, Higgs E, Harris JA. 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24:599–605

Hoffmann AA, Weeks AR. 2007. Climatic selection on genes and traits after a 100 year-old invasion: a critical look at the temperate-tropical clines in *Drosophila melanogaster* from eastern Australia. *Genetica* 129:133–47

Hoffmann AA, Willi Y. 2008. Detecting genetic responses to environmental change. *Nat. Rev. Genet.* 9:421–32

Holt RD. 1996. Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. *Evol. Ecol.* 10:1–11

Holt RD. 2003. On the evolutionary ecology of species' ranges. *Evol. Ecol. Res.* 5:159–78

Holt RD, Barfield M. 2009. Trophic interactions and range limits: the diverse roles of predation. *Proc. R. Soc. B* 276:1435–42

Hubbell SP. 2001. *A Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton Univ. Press

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008a. Ecological consequences of genetic diversity. *Ecol. Lett.* 11:609–23

Hughes AR, Stachowicz JJ. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci. USA* 101:8998–9002

Stresses the view that to understand ecological dynamics, one must also consider rapid evolution.

Hughes GO, Thuiller W, Midgley GF, Collins K. 2008b. Environmental change hastens the demise of the critically endangered riverine rabbit (*Bunolagus monticularis*). *Biol. Conserv.* 141:23–34

Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22:415–27

Ives AR, Cardinale BJ. 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* 429:174–77

Jackson ST, Overpeck JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26:194–220

Jakob SS, Ihlow A, Blattner FR. 2007. Combined ecological niche modelling and molecular phylogeography revealed the evolutionary history of *Hordeum marinum* (Poaceae)—niche differentiation, loss of genetic diversity, and speciation in Mediterranean Quaternary refugia. *Mol. Ecol.* 16:1713–27

Jeltsch F, Moloney KA, Schurr F, Köchy M, Schwager M. 2008. The state of plant population modelling in light of environmental change. *Perspect. Plant Ecol. Evol. Syst.* 9:171–89

Jiang L, Tan J, Pu Z. 2010. An experimental test of Darwin's naturalization hypothesis. *Am. Nat.* 175:415–23

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

Johnson MTJ, Lajeunesse MJ, Agrawal AA. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* 9:24–34

Johnson MTJ, Stinchcombe JR. 2007. An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.* 22:250–57

Jones LE, Becks L, Ellner SP, Hairston NG, Yoshida T, Fussmann GF. 2009. Rapid contemporary evolution and clonal food web dynamics. *Philos. Trans. R. Soc. B* 364:1579–91

Juliano SA, Lounibos LP, Nishimura N, Greene K. 2010. Your worst enemy could be your best friend: predator contributions to invasion resistance and persistence of natives. *Oecologia* 162:709–18

Jump AS, Hunt JM, Martinez-Izquierdo JA, Peñuelas J. 2006a. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Mol. Ecol.* 15:3469–80

Jump AS, Hunt JM, Peñuelas J. 2006b. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Change Biol.* 12:2163–74

Jump AS, Peñuelas J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8:1010–20

Kawecki TJ. 2008. Adaptation to marginal habitats. *Annu. Rev. Ecol. Evol. Syst.* 39:321–42

Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12:334–50

Kearney M, Porter WP, Williams C, Ritchie S, Hoffmann AA. 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Funct. Ecol.* 23:528–38

Kembel SW. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecol. Lett.* 12:949–60

Kembel SW, Hubbell SP. 2006. The phylogenetic structure of a neotropical forest tree community. *Ecology* 87: S86–99

Kinnison MT, Hairston NG. 2007. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Funct. Ecol.* 21:444–54

Kinnison MT, Unwin MJ, Quinn TP. 2008. Eco-evolutionary vs. habitat contributions to invasion in salmon: experimental evaluation in the wild. *Mol. Ecol.* 17:405–14

Kirkpatrick M, Barton NH. 1997. Evolution of a species' range. *Am. Nat.* 150:1–23

Klanderud K, Totland O. 2007. The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos* 116:1279–88

Klironomos JN. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70

Kokko H, López-Sepulcre A. 2007. The ecogenetic link between demography and evolution: can we bridge the gap between theory and data? *Ecol. Lett.* 10:773–82

Kondoh M. 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299:1388–91

Provides, to date, the most promising attempt to develop mechanistic models of species distribution.

Kraft NJB, Cornwell WK, Webb CO, Ackerly D. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am. Nat.* 170:271–83

Kramer K, Degen B, Buschbom J, Hickler T, Thuiller W, et al. 2010. Modelling exploration of the future of European beech (*Fagus sylvatica L.*) under climate change—ange, abundance, genetic diversity and adaptive response. *Forest Ecol. Manag.* 259:2213–22

Kullman L. 2006. Long-term geobotanical observations of climate change impacts in the Scandes of West-Central Sweden. *Nord. J. Bot.* 24:445–67

Kuparinen A, Schurr FM. 2007. A flexible modelling framework linking the spatio-temporal dynamics of plant genotypes and populations: application to gene flow from transgenic forests. *Ecol. Model.* 202:476–86

Lankau RA. 2009. Genetic variation promotes long-term coexistence of *Brassica nigra* and its competitors. *Am. Nat.* 174:E40–53

Lankau RA, Strauss SH. 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* 317:1561–63

Lavergne S, Debussche M, Thompson JD. 2005a. Limitations on reproductive success in endemic *Aquilegia viscosa* (Ranunculaceae) relative to its widespread congener *A. vulgaris*: the interplay of herbivory and pollination. *Oecologia* 142:212–20

Lavergne S, Molina J, Debussche M. 2006. Fingerprints of environmental change on the rare Mediterranean flora: a 115-year study. *Glob. Change Biol.* 12:1466–78

Lavergne S, Molofsky J. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc. Natl. Acad. Sci. USA* 104:3883–88

Lavergne S, Thuiller W, Molina J, Debussche M. 2005b. Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115 year study in the Mediterranean region. *J. Biogeogr.* 32:799–811

Leibold MA, McPeek MA. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–410

le Roux PC, McGeoch MA. 2008. Rapid range expansion and community reorganization in response to warming. *Glob. Change Biol.* 14:2950–62

Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ. 2006. TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecol. Model.* 199:409–20

Loreau M, Mouquet N, Gonzalez A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. USA* 100:12765–70

Losos JB. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11:995–1003

Lovette IJ, Hochachka WM. 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology* 87: S14–28

Lynch M, Lande R. 1993. Evolution and extinction in response to environmental change. In *Biotic Interactions and Global Change*, ed. P Kareiva, JG Kingsolver, RB Huey, pp. 234–50. Sunderland, MA: Sinauer Assoc.

MacArthur RH. 1955. Fluctuation of animal population and a measure of community stability. *Ecology* 36:533–36

Massot M, Clobert J, Ferriere R. 2008. Climate warming, dispersal inhibition and extinction risk. *Glob. Change Biol.* 14:461–69

May RM. 1974. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton Univ. Press

Medley KA. 2010. Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Glob. Ecol. Biogeogr.* 19:122–33

Memmott J, Craze PG, Waser NM, Price MV. 2007. Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.* 10:710–17

Midgley GF, Hughes GO, Thuiller W, Rebelo AG. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Divers. Distrib.* 12:555–62

Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P. 2008. Bird migration times, climate change, and changing population sizes. *Glob. Change Biol.* 14:1959–72

Miller-Rushing AJ, Primack RB. 2008. Global warming and flowering times in Thoreau's concord: a community perspective. *Ecology* 89:332–41

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, et al. 2006. Biotic interactions and plant invasions. *Ecol. Lett.* 9:726–40

Molofsky J, Bever JD. 2002. A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. *Proc. R. Soc. Lond. Ser. B* 269:2389–93

Moore JS, Hendry AP. 2009. Can gene flow have negative demographic consequences? Mixed evidence from stream threespine stickleback. *Philos. Trans. R. Soc. B* 364:1533–42

Morin X, Augspurger C, Chuine I. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? *Ecology* 88:2280–91

Morin X, Thuiller W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90:1301–13

Morin X, Viner D, Chuine I. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *J. Ecol.* 96:784–94

Mouquet N, Leadley P, Meriguet J, Loreau M. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos* 104:77–90

Münkemüller T, Reineking B, Travis J, Bugmann H, Johst K. 2009. Disappearing refuges in time and space: how environmental change threatens species coexistence. *Theor. Ecol.* 2:217–27

Nuismer SL, Kirkpatrick M. 2003. Gene flow and the coevolution of parasite range. *Evolution* 57:746–54

Orr HA, Unckless RL. 2008. Population extinction and the genetics of adaptation. *Am. Nat.* 172:160–69

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

Palkovacs EP, Marshall MC, Lamphere BA, Lynch BR, Weese DJ, et al. 2009. Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philos. Trans. R. Soc. B* 364:1617–28

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37:637–69

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42

Pearman PB, Guisan A, Broennimann O, Randin CF. 2008. Niche dynamics in space and time. ***Trends Ecol. Evol.*** **23:149–58**

Pease CP, Lande R, Bull JJ. 1989. A model of population growth, dispersal and evolution in a changing environment. ***Ecology*** **70:1657–64**

Pelletier F, Clutton-Brock T, Pemberton J, Tuljapurkar S, Coulson T. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. *Science* 315:1571–74

Perron GG, Gonzalez A, Buckling A. 2008. The rate of environmental change drives adaptation to an antibiotic sink. *J. Evol. Biol.* 21:1724–31

Peterson AT, Nyari AS. 2008. Ecological niche conservatism and pleistocene refugia in the thrush-like mourner, Schiffornis sp., in the neotropics. *Evolution* 62:173–83

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

Phillips BL. 2009. The evolution of growth rates on an expanding range edge. *Biol. Lett.* 5:802–4

Phillips BL, Shine R. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proc. Natl. Acad. Sci. USA* 101:17150–55

Polechova J, Barton N, Marion G. 2009. Species' range: adaptation in space and time. *Am. Nat.* 174:E186–204

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**

Post E, Pedersen C. 2008. Opposing plant community responses to warming with and without herbivores. *Proc. Natl. Acad. Sci. USA* 105:12353–58

Price TD, Kirkpatrick M. 2009. Evolutionarily stable range limits set by interspecific competition. *Proc. R. Soc. Lond. B* 276:1429–34

Prinzing A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. Ser. B* 268:1–7

Stresses that species niches are changing over space and time and that models must account for this.

Is the first model to show the interplay of migration and adaptation in tracking environmental changes through space and time.

Discusses how interactions between species evolution and ecological interactions are potentially widespread.

Prinzing A, Reiffers R, Braakhekke WG, Hennekens SM, Tackenberg O, et al. 2008. Less lineages—more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecol. Lett.* 11:808–19

Pyron RA, Burbrink FT. 2009. Lineage diversification in a widespread species: roles for niche divergence and conservatism in the Common Kingsnake, *Lampropeltis getula*. *Mol. Ecol.* 18:3443–57

Qian H, Ricklefs RE. 2004. Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. *J. Ecol.* 92:253–65

Ramirez-Valiente JA, Lorenzo Z, Soto A, Valladares F, Gil L, Aranda I. 2009. Elucidating the role of genetic drift and natural selection in cork oak differentiation regarding drought tolerance. *Mol. Ecol.* 18:3803–15

Reusch TBH, Ehlers A, Hammerli A, Worm B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci. USA* 102:2826–31

Reusch TBH, Wood TE. 2007. Molecular ecology of global change. *Mol. Ecol.* 16:3973–92

Revell LJ, Harmon LJ, Collar DC. 2008. Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* 57:591–601

Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448:925–29

Reznick DN, Ghalambor CK. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112:183–98

Ricklefs RE, Latham RE. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *Am. Nat.* 139:1305–21

Robinson BW, Parsons KJ. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Can. J. Fish. Aquat. Sci.* 59:1819–33

Rodder D, Lotters S. 2009. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Glob. Ecol. Biogeogr.* 18:674–87

Rodríguez-Sánchez F, Arroyo J. 2008. Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. *Glob. Ecol. Biogeogr.* 17:685–95

Saccheri I, Hanski I. 2006. Natural selection and population dynamics. *Trends Ecol. Evol.* 21:341–47

Sarup P, Frydenberg J, Loeschcke V. 2009. Local adaptation of stress related traits in *Drosophila* buzzatii and *Drosophila* simulans in spite of high gene flow. *J. Evol. Biol.* 22:1111–22

Savolainen O, Pyhajarvi T, Knurr T. 2007. Gene flow and local adaptation in trees. *Annu. Rev. Ecol. Evol. Syst.* 38:595–619

Schluter D. 2000. *The Ecology of Adaptive Radiation*. Oxford: Oxford Univ. Press

Schweiger O, Settele J, Kudrna O, Klotz S, Kuhn I. 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89:3472–79

Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* 40:415–36

Skelly DK, Joseph LN, Possingham HP, Freidenburg LK, Farrugia TJ, et al. 2007. Evolutionary responses to climate change. *Conserv. Biol.* 21:1353–55

Slobodkin LB. 1961. *Growth and Regulation of Animal Populations*. New York: Holt, Rinehart & Winston

Smith SA, Beaulieu JM. 2009. Life history influences rates of climatic niche evolution in flowering plants. *Proc. R. Soc. Lond. B* 276:4345–52

Stewart JR. 2009. The evolutionary consequence of the individualistic response to climate change. *J. Evol. Biol.* 22:2363–75

Stockwell CA, Hendry AP, Kinnison MT. 2003. Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* 18:94–101

Stokes KE, Buckley YM, Sheppard AW. 2006. A modelling approach to estimate the effect of exotic pollinators on exotic weed population dynamics: bumblebees and broom in Australia. *Divers. Distrib.* 12:593–600

Strauss SY, Lau JA, Carroll SP. 2006. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? *Ecol. Lett.* 9:354–71

Tallmon DA, Luikart G, Waples RS. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends Ecol. Evol.* 19:489–96

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, et al. 2001a. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–81

Reviews most studies showing rapid evolution as a response to climate change.

Stresses that species evolution can directly affect population dynamics and persistence.

Provides a comprehensive review of theoretical and empirical aspects of the ecological and evolutionary limitation of species ranges.

Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR. 2001b. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291:2598–600

Thompson JN. 2005. *The Geographic Mosaic of Coevolution*. Chicago: Univ. Chicago Press

Thuiller W, Albert C, Araujo MB, Berry PM, Cabeza M, et al. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspect. Plant Ecol. Evol. Syst.* 9:137–52

Thuiller W, Albert C, Dubuis A, Randin C, Guisan A. 2010a. Variation in habitat suitability does not always relate to variation in species' plant functional traits. *Biol. Lett.* 6:120–23

Thuiller W, Gallien L, Boulangeat I, de Bello F, Münkemüller T, et al. 2010b. Resolving Darwin's naturalization conundrum: a quest for evidence. *Divers. Distrib.* 16:461–75

Thuiller W, Lavorel S, Araujo M, Sykes MT, Prentice IC. 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. USA* 102:8245–50

Thuiller W, Slingsby JA, Privett SDJ, Cowling RM. 2007. Stochastic species turnover and stable coexistence in a fire-prone plant community. *PloS One* 2:e938

Tingley MW, Monahan WB, Beissinger SR, Moritz C. 2009. Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. USA* 106:19637–43

Trussell GC, Smith LD. 2000. Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. *Proc. Natl. Acad. Sci. USA* 97:2123–27

Urban MC, Phillips BL, Skelly DK, Shine R. 2007. The cane toad's (*Chaunus* [*Bufo*] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proc. R. Soc. Lond. B* 274:1413–19

Vamosi SM, Heard SB, Vamosi JC, Webb CO. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.* 18:572–92

Van Doorslaer W, Stoks R, Duvivier C, Bednarska A, De Meester L. 2009. Population dynamics determine genetic adaptation to temperature in *Daphnia*. *Evolution* 63:1867–78

van Heerwaarden B, Kellermann V, Schiffer M, Blacket M, Sgro CM, Hoffmann AA. 2009. Testing evolutionary hypotheses about species borders: patterns of genetic variation towards the southern borders of two rainforest *Drosophila* and a related habitat generalist. *Proc. R. Soc. Lond. B* 276:1517–26

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

Vellend M, Harmon LJ, Lockwood JL, Mayfield MM, Hughes AR, et al. 2007. Effects of exotic species on evolutionary diversification. *Trends Ecol. Evol.* 22:481–88

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

Visser ME, Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. Lond. B* 272:2561–69

Vourc'h G, Martin JL, Duncan P, Escarre J, Clausen TP. 2001. Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. *Oecologia* 126:84–93

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33:475–505

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7:510–23

Whitlock R, Grime JP, Booth R, Burke T. 2007. The role of genotypic diversity in determining grassland community structure under constant environmental conditions. *J. Ecol.* 95:895–907

Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36:519–39

Wipf S, Rixen C, Mulder CPH. 2006. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Glob. Change Biol.* 12:1496–506

Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. USA* 96:1463–68

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

Zheng CZ, Ovaskainen O, Hanski I. 2009. Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Philos. Trans. R. Soc. B* 364:1519–32