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COMMUNITY ASSEMBLY, NICHE CONSERVATISM, AND ADAPTIVE EVOLUTION IN CHANGING ENVIRONMENTS

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The widespread correspondence between phenotypic variation and environmental conditions, the “fit” of organisms to their environment, reflects the adaptive value of plant functional traits. Several processes contribute to these patterns: plasticity, ecological sorting, and adaptive evolution. This article addresses the importance of ecological sorting processes (community assembly, migration, habitat tracking, etc.) as primary causes of functional trait distributions at the local and landscape level. In relatively saturated communities, plants will establish and regenerate in environments to which they are well adapted, so their distributions, and the distributions of associated functional traits, will reflect the distribution of optimal or near-optimal environmental conditions in space and time. The predicted evolutionary corollary of this process is that traits related to habitat occupancy, e.g., environmental tolerances, will be under stabilizing selection. This process contributes to the widely observed pattern of phylogenetic niche conservatism, i.e., ecological and phenotypic similarities of closely related species. Evidence for niche conservatism in plants is reviewed. Based on Jackson and Overpeck’s concept of the realized environment, I propose three scenarios in which a species’ distributional responses to environmental conditions will lead to a “mismatch” between its environmental tolerances and the environments it occupies, thus creating opportunities for adaptive evolution: (1) the colonization of “environmental islands” (habitats that are discontinuous in niche space) that require large adaptive shifts in tolerance of one or more environmental factors; (2) the persistence of “trailing-edge” populations in species tracking changing climate, if barriers to dispersal of competitors prevent competitive exclusion in the deteriorating conditions; and (3) responses to changes in the realized environment in multidimensional niche space, in which species are predicted to track environmental factors for which they exhibit narrow tolerances and exhibit adaptive evolutionary response along axes where they exhibit greater niche breadth. These three scenarios provide a conceptual framework that emphasizes the role of ecological sorting processes and stabilizing selection as the context for understanding opportunities for adaptive evolution in heterogeneous and changing environments.

Keywords: adaptation, California flora, climate change, community assembly, environmental tolerances, niche, phylogeny, specific leaf area, stabilizing selection.

1. Introduction

Plant functional traits are directly responsible for the acquisition of resources required for growth (light, water, nutrients, CO₂) and the regulation of conditions that influence metabolism (e.g., temperature, turgor pressure). Functional traits vary across a wide range of spatial and temporal scales and among cells, leaves, shoots, individuals, populations, and ecosystems. Functional traits are considered adaptive if the phenotype occurring in a particular environment enhances performance in that environment (e.g., improved resource acquisition, growth, survival and/or reproduction) relative to alternative phenotypic states. Familiar examples include carbon gain of shade versus sun leaves in contrasting light environments, contrasting allocation strategies related to resource availability, and variation in leaf size and angle with respect to radiation and water availability.

The widespread correspondence between phenotypic vari-

ation and environmental conditions (i.e., the state of adapt- edness) reflects the adaptive value of functional traits. For example, leaf size commonly increases with water availability, and this pattern may be observed among individuals (Sultan and Bazzaz 1993), species (Cunningham et al. 1999), and community assemblages (Dolph and Dilcher 1980; Fonseca et al. 2000). Depending on the scale of analysis, these patterns reflect one or more of three interacting processes: (1) phenotypic plasticity: the modification of the phenotype during development in response to the environment (Sultan 1987); (2) ecological sorting: the differential success, due to their functional characteristics, of populations or species in contrasting environments (Weiher and Keddy 1995); (3) adaptation by natural selection: heritable changes in the phenotype in populations occupying different environments, as a result of the adaptive value of the trait (Cody and Mooney 1978).

As all heritable differences among species are ultimately traceable to evolutionary events, it is tempting to give natural selection a primary role compared with the other two processes. This temptation is reinforced by the idea that evolution provides the “ultimate” cause of phenotypic variation, in con-

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trast to “proximate” developmental and ecological causes (Mayr 1982). This view, however, obscures the fact that all three processes (phenotypic plasticity, ecological sorting, and natural selection) contribute to the observed distribution of form and function in the natural world.

This article addresses the relationship between natural selection and ecological sorting processes to understand the evolution of plant functional traits. To do so, we must reconcile two sets of empirical observations. On the one hand, we know that natural selection can be extraordinarily powerful, leading to rapid change in phenotypes and local adaptation of populations in contrasting environments. Adaptive radiations and divergence between close relatives provide dramatic examples, as illustrated by the rapid and repeated evolution of woodiness in herbaceous lineages colonizing oceanic islands (Carlquist 1974; Givnish 1998). On the other hand, comparative analysis of ecological variation frequently reveals a high degree of evolutionary conservatism, or phylogenetic niche conservatism. A high degree of phenotypic and ecological similarity between closely related species or lineages implies that there has been little evolutionary change since the species’ divergence from a common ancestor or that parallel evolutionary changes have occurred independently since divergence. The fossil record also provides abundant evidence of evolutionary stasis, a key observation in the development of the theory of punctuated evolution (Eldredge and Gould 1972; Gould 2002). In the simplest terms, the absence of evolutionary change may result from one or more of three causes: (1) insufficient time, relative to rates of evolution; (2) lack of appropriate genetic variation for the traits in question (Bradshaw 1991) (this is used in the broad sense to include developmental constraints; Maynard Smith et al. 1985); (3) stabilizing selection that favors intermediate trait values and thus maintains ancestral states (optimizing selection; *sensu* Travis 1989). Contrasting patterns of directional selection among conspecific populations, or short-term fluctuations in directional selection over time, may appear as stabilizing selection at the species level (Eldredge 1995).

Bradshaw (1991) has argued that the absence of appropriate genetic variation can be a significant factor influencing patterns and rates of evolution in local populations. However, quantitative genetic studies have generally documented fairly high heritability for quantitative traits of ecological significance (Geber and Griffen 2003). Ecotypic differentiation (Clausen et al. 1948), niche differentiation among close relatives (Silvertown et al. 2000), and adaptive radiation in lineages “released” on oceanic islands (Givnish 1998) also indicate that the absence of appropriate genetic variation is an unlikely explanation for long-term stasis in plant function. Stabilizing selection has thus been suggested as a factor of central importance in the evolution of ecological traits (Travis 1989; Harvey and Pagel 1991; Lord et al. 1995). In an ecological context, community assembly and habitat tracking processes may be critical to promoting stabilizing selection. In the assembly and reshuffling of ecological communities, competing species will preferentially occupy habitats and microsites that most closely match conditions to which they were previously adapted (the optimal conditions for their establishment and regeneration). This sorting process, insofar as it allows species to track favored habitats rather than adapt to new ones, promotes stabilizing selection and is predicted to lead to niche

conservatism through evolutionary time (Harvey and Pagel 1991; Eldredge 1995; Webb et al. 2002). Others have proposed a similar argument with regard to phenotypic plasticity, as adjustments in the phenotype enhance performance of individuals and genotypes in heterogeneous environments and potentially reduce the strength of selection within populations (Bradshaw 1965; Sultan 1987; see Donohue 2003).

The objective of this article is to examine the evidence and implications of this hypothesis for understanding the evolution of functional traits. I first consider the ecological evidence that community assembly processes and habitat tracking are significant factors that contribute to the observed “fit” between organismal traits and the environment, in space (sec. 2) and time (sec. 3). I then examine the link between these ecological processes and stabilizing selection more closely (sec. 4) and review the empirical evidence for evolutionary conservatism in plant functional traits (sec. 5). Here, I draw on several case studies from recent work in my lab that has focused on the ecology and evolution of the mediterranean climate chaparral flora of California. Finally, in an attempt to reconcile evidence for the evolutionary stasis in plant functional traits and the power of natural selection in local adaptation, I consider several conceptual models relating niche theory, community assembly, and natural selection (sec. 6). These models indicate distinct scenarios in which the match between organisms and their optimal conditions may break down and adaptive evolutionary change may be expected to occur. The predictions of the models point to some nonintuitive relationships between dispersal ability, niche breadth, and adaptive evolution in heterogeneous and changing environments.

2. Community Assembly and the Distribution of Plant Functional Traits

In heterogeneous environments on small spatial scales, the distribution of plant species reflects the influence of abiotic filters and biotic interactions, collectively referred to as the community assembly process (Weiher and Keddy 1999). From a phytocentric perspective, a “small” spatial scale may be defined as the scale at which there is effectively no dispersal limitation influencing the distribution of species over several generations. In other words, over several generations, propagules from every species in the local species pool could have reached each spot in the landscape. The observed species distribution at this scale will thus reflect the filters created by seed germination, seedling establishment, physiological tolerances, demographic effects of disturbance events, competition with other species in the community, and the biotic interactions with herbivores, pathogens, and mutualists (Bazzaz 1991; Weiher and Keddy 1995, 1999; Zobel 1997; Díaz et al. 1998). These assembly processes lead to the differential distribution of species and significant associations between environmental conditions and the species’ functional traits.

A recent example from my lab addressed the distribution of shrub species and associated leaf traits on north- to south-facing slopes in a northern California chaparral (Ackerly et al. 2002). Characteristic of semiarid ecosystems, the difference in solar exposure on equatorial and polar-facing slopes (south- and north-facing, respectively) dramatically impacts thermal regimes and moisture balance, resulting in distinctive plant

communities. The local topography of the research site (Jasper Ridge Biological Preserve, San Mateo County, Calif.) creates a series of parallel drainages that result in an interstitial pattern of species distributions on alternating north- and south-facing slopes. These patchy distributions on the scale of 10^1 – 10^3 m provide evidence that, at this site, dispersal limitation is not a significant factor in species distributions on time scales of several generations. Effects of slope and aspect can be quantified using a measure of potential solar insolation (incident solar radiation) derived from a Geographic Information System base map. Species distributions in relation to this measure present a classical Gleasonian picture of independent niche distributions along an environmental gradient (fig. 1a).

Based on these patterns, we then asked whether the species' positions along the gradient were associated with either of two aspects of leaf function: specific leaf area (SLA) and leaf size (not discussed here). As expected from comparative and functional studies (Parsons and Moldenke 1975; Givnish 1979; Cunningham et al. 1999; Fonseca et al. 2000; Lamont et al. 2002), there were trends toward lower SLA (thicker or denser leaf tissue) in species preferring high-insolation, south-facing slopes (fig. 1b). Moreover, when species SLA values were averaged for plots occurring at different points along the gradient, the interspecific pattern resulted in a tight, linear correlation between insolation and mean SLA at the community level (fig. 1c).

Comparing the patterns in the interspecific and community-level data provides valuable insights into community structure. Species with high SLA are generally deciduous with high photosynthetic rates (Mooney and Dunn 1970; Reich et al. 1997), and this functional strategy is often associated with disturbance-dependent regeneration (Ackerly, in press). But the decline in mean SLA with insolation is not due to a shift from a deciduous to an evergreen community. Rather, both leaf types are widely distributed across the gradient, and in both deciduous and evergreen species SLA declines in parallel. Note that these analyses were conducted using species mean values for SLA, minimizing the role of phenotypic plasticity across the gradient. Plasticity within species also leads to lower SLA at higher insolation. The combined effects of plasticity and species turnover would lead to even stronger shifts in leaf traits across this gradient.

These patterns in functional trait distributions at the local scale are also observed at larger spatial scales. Classic examples include the convergent patterns in frequency of deciduous versus evergreen leaf habit along seasonality gradients (Mooney et al. 1970; Reich 1995) and the frequency of species with the C_4 photosynthetic pathway in relation to temperature and precipitation (review Hattersley 1983). Paleoecologists have examined leaf physiognomy (focusing on traits that are preserved in macrofossil assemblages) in relation to climate (Bailey and Sinnott 1915, 1916; Wolfe 1990, 1995). The most significant results to emerge from these studies are the positive correlation between leaf size and precipitation (annual or growing season) and the strong, but poorly understood, negative relationship between the frequency of toothed leaf margins and mean annual temperature (Baker-Brosh and Peet 1997; Wilf 1997). On a global scale, the relationships between plant form and climate have played a pivotal role in the development of plant ecology (Schimper 1903; Warming 1909; Box 1981).

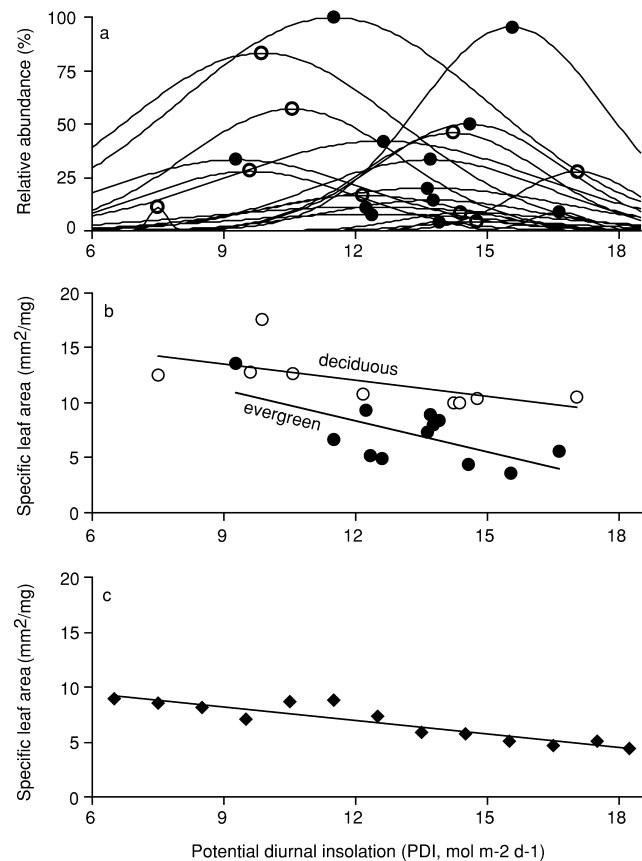


Fig. 1 a, Distributions of 22 chaparral plant species along gradients of potential diurnal solar radiation across north- and south-facing slopes. Niche optima and tolerances along this gradient calculated from actual distributions (see Ackerly et al. 2002) have been illustrated as Gaussian responses, although several species exhibited monotonic or bimodal distributions. Positions of niche optima show deciduous (open circles) versus evergreen (filled circles) species. b, Scatterplot of species mean specific leaf area (SLA, leaf area/mass) versus niche optimum along the insolation gradient. Symbols and regression lines shown separately for deciduous versus evergreen species. c, Mean SLA for co-occurring species in plots along the gradient (means weighted by relative cover values for each species). Note that the mean pattern at the community level is much tighter, but shallower, than the underlying correlation at the species level. Modified from Ackerly et al. (2002) with permission.

There are also strong relationships between direct measures of physiological tolerance (e.g., to temperature and water availability) and plant distributions (review Woodward 1987). Examples include the reduction in temperature optima for photosynthesis in species arrayed along elevational gradients (Pisek et al. 1973) and increased drought tolerance in species that experience greater water deficit (Pockman and Sperry 2000). The influence of physiological tolerances on species distributions has been emphasized primarily at the “stressful” edge (e.g., cold or dry) of species ranges (Woodward 1987).

The realized niche, in relation to climate parameters, reflects the cumulative effects of physiological tolerances and biotic interactions operating throughout the individual’s life cycle. The realized climatic niche can be estimated directly by map-

ping species distribution data onto climate diagrams (Austin et al. 1990; Peterson et al. 1999; Moody and Meentemeyer 2001). Such analyses offer great potential for relating morphological or physiological traits to species distributions, as in the small-scale analysis of the Jasper Ridge community above. In another example, at a larger scale in the California flora, we found a significant reduction in maximum genome size associated with realized niche distributions at extreme temperatures (both hot and cold) (Knight and Ackerly 2002). Significantly, similar patterns were observed in alien and native species. Since the alien species have been present for less than 200 yr, these patterns clearly reflect the influence of intrinsic physiological traits on distributions (apparently correlated with genome size), rather than the evolution of genome size in relation to climate.

There are two noteworthy aspects of the patterns discussed above. First, while the trait means, or relative frequencies, shift along environmental gradients, there is considerable functional diversity within local communities at each point. This reflects the fact that **species with widely varying functional traits co-exist under similar macroclimate conditions** (Givnish 1987; Westoby et al. 2002; Cornwell and Ackerly 2003). The classical interpretation for this pattern is that **the coexistence results from niche partitioning of heterogeneous environments within the community**. For example, in the shrub distributions at Jasper Ridge, the overall variation in SLA observed in the community as a whole reflects microhabitat partitioning at a smaller scale along topographic gradients. Colonization-competition trade-offs, a result of contrasting ecological characteristics of pioneer versus persistent, late-successional species, may also play a large role in maintaining plant diversity (Tilman 1994) and thus help maintain high levels of trait diversity within communities (Grime 1977; Bazzaz 1979; Rees and Westoby 1997). In contrast to explicit niche models, the microhabitat variable underlying colonization-competition trade-offs is simply the time since disturbance; as a result, species traits would not be correlated with structural components of microhabitat (topography, soil type), although they may show correlations with environmental factors like light and soil nutrients that change during the disturbance-colonization process (Tilman 1988).

These two models for coexistence can explain the shifts in mean trait values along an environmental gradient, assuming that individual species exhibit contrasting optima in relation to microhabitat or life history specialization (e.g., shallow vs. deep rooted; colonizer vs. competitor), and that these optima shift in relation to macroclimate, leading to a shift in the entire trait distribution at the community level (Westoby et al. 1998). If this explanation is correct, then the interspecific variation in functional traits within communities is consistent with the view that ecological sorting results in a close match between functional traits, niche optima, and species distributions at a range of spatial scales.

The second point is that at large spatial scales it becomes increasingly difficult to separate the roles of ecological sorting and evolutionary adaptation as explanations for the match between species traits and environment. Studies conducted on small spatial scales, like the Jasper Ridge study discussed above, are valuable because we can safely conclude that local adaptation has played a minimal role in small-scale trait-

environment relationships. While local adaptation may be ongoing, the adjustments that occur within species are small compared to interspecific differences that are the primary contributor to community-level patterns. In addition, the patchy distribution of individual species in heterogeneous landscapes (e.g., north- vs. south-facing slopes) is clearly a reflection of sorting processes alone and not independent adaptation of the same species to each patch. At large spatial scales, plasticity and local adaptation may be important factors within species. However, it is still safe to say that community-level shifts in physiognomy are driven primarily by changes in species composition along environmental gradients (due to individualistic differences in environmental tolerances), and evolutionary differentiation within species is small relative to the large and evolutionarily conserved differences among species.

3. Paleoecology and the Assembly of Plant Communities

Paleoecological research has provided enormous insights into the history of biotic migrations and the role of community assembly in shaping large-scale distributions of plant species and communities. The response of vegetation to climate change provides compelling evidence of the reshuffling of plant communities and the rapid rates of geographic migration on time scales of thousands to tens of millions of years (Graham 1999). The Quaternary history of forests in Europe and North America has been studied in particular detail, based on an extensive pollen record documenting distributional shifts of hundreds of kilometers since the last glacial maximum ~18,000 years before present (Webb 1988; Huntley 1990b). A central question regarding these migrations is whether plant species maintain a close equilibrium with their optimal climatic range (the dynamic equilibrium hypothesis), or whether plant distributions lag behind changing climate (the disequilibrium hypothesis). The answer to this question depends on the temporal and spatial scale of analysis and the relationship between geographic gradients in climate, temporal rates of climate change, and potential rates of plant migration (Webb 1986; Prentice et al. 1991).

The northward migration of tree species is estimated at 100–1000+ m/yr (Huntley 1991). Assuming a prereproductive period of 5–10 yr and constraints on the rate of population growth, this migration rate requires even longer dispersal events in each generation (Clark et al. 1998). In the Quaternary, these rates appear to be sufficient to maintain vegetation in equilibrium with climate on time scales of several thousand years, although transient disequilibria may occur over shorter intervals (Prentice et al. 1991). In addition, contrasting rates and directions of migration provide extensive evidence of individualistic responses in species distributions due to variation in tolerance for different components of the changing climate. This diversity in the responses of different species has led to shifting community composition, including the appearance of “no-analogue” communities with species combinations not observed in modern vegetation (Overpeck et al. 1985; Huntley 1990a; Jackson and Overpeck 2000). The distribution of these communities parallels the occurrence of no-analogue climatic conditions (combinations of abiotic conditions that do not occur in the modern landscape), as predicted by the dynamic

equilibrium model of vegetation-climate relationships (Williams et al. 2001).

Ideally, paleoecological data would allow us to examine the relationships between plant distributions, functional traits, and climate over time, analogous to the patterns in space discussed in section 2. This is not always possible over long time scales, as plant and animal distributions are often used as the basis for paleoclimate reconstruction. The nearest living relative (NLR) method uses present distributions (assuming equilibrium with climate) to determine physiological tolerances of different species. Then, by assuming evolutionary stasis in these tolerances, past climates can be inferred based on species assemblages in paleocommunities (Graham 1999; Tiffney and Manchester 2001). To avoid circularity, paleoclimate may be reconstructed using one set of indicator species, and then distributional changes can be evaluated in an independent group of species (Prentice et al. 1991). This approach, combined with nonbiotic sources of climate reconstruction, has generally confirmed the validity of the NLR approach. In addition, for Quaternary vegetation, the short time frame relative to generation times of the trees makes the assumption of stasis less problematic. That migration rates are sufficiently high to maintain equilibrium with environmental factors on time scales of $>10^3$ yr, even in long-lived organisms experiencing rapid climate change, is an important factor that promotes evolutionary stasis. Thus, the history of plant responses to climate change provides broad support for the view that environmental tolerances evolve very slowly (sec. 5 on niche conservatism).

The alternative to the NLR method of paleoclimate reconstruction is the analysis of leaf physiognomy in macrofossil assemblages (Wolfe 1995; Wilf 1997). Validation studies for this method have evaluated extant communities across broad climatic gradients and, as noted above, have found two particularly strong relationships: a positive correlation between mean leaf size and either annual or growing-season precipitation and a negative correlation between the frequency of toothed leaves and mean annual temperature. The extant data set provides an excellent example of the relationship between plant form and climate in the present, but given the large spatial scale, it is impossible to unambiguously separate the contributions of adaptive evolution and ecological sorting processes. Independent analyses of paleoclimates that do not rely on physiognomy will be needed before the macrofossil data can be used as strong tests of the relationships between plant form and climate.

In sum, the paleoecological record provides critical evidence of the potential rate of plant migrations and strong support for the dynamic equilibrium view that species distributions track climatic conditions on continental scales. This evidence is essential to the overall argument of this article, as it strongly supports the view that landscape and continental patterns in the relationships between plant functional traits, physiological tolerances, and species distributions are strongly influenced by ecological processes of migration and community assembly. Certainly, adaptive evolution may be occurring in tandem with these ecological sorting processes; differentiation between related species demonstrates that adaptive evolution is widespread, although it proceeds at a sufficiently modest pace to preserve the phylogenetic signal of niche conservatism (sec. 5). The role of ecological processes is highlighted here to empha-

size their contribution to the “adaptive” relationships between plant form and environment and to underline their potential role in promoting stabilizing selection and thus influencing rates of evolution.

I hope that the discussion above provides a convincing case for the importance of community assembly processes in plant evolution. Imagine how different the evolutionary record and modern vegetation would look if the world were divided into hundreds of small floras with extreme dispersal limitation between them, so that local plant-environment relationships were driven almost entirely by adaptive evolution within each flora. That the earth is dominated by continental landmasses that facilitate large-scale biotic migrations is a contingent feature of geologic history with profound importance for evolution and the history of ecological communities.

4. Community Assembly, Habitat Tracking, and Natural Selection

The central premise of the argument relating ecological sorting processes to stabilizing selection is that a species that can track favorable conditions in space and time will not experience strong selection for adaptive modification of environmental tolerances. It is interesting, and perhaps not surprising, that this argument has been advanced most forcefully by paleontologists in an effort to understand the factors promoting stasis in the fossil record (Vrba 1985; Vermeij 1987; Eldredge 1989, 1995; Gould 2002). Armed with extensive evidence of distributional shifts in response to climate change, paleontologists have been particularly receptive to the evolutionary importance of these large-scale ecological phenomena. Habitat tracking has thus been lumped under the broad heading of “non-Darwinian” arguments connected to the debate over phyletic gradualism versus punctuated equilibrium (Williams 1992; Eldredge 1995; Gould 2002). As an ecologist, I find it rather disconcerting that this synthesis of community ecology with natural selection could be seen as non-Darwinian. These arguments, as presented in this article, are built on theories of niche differentiation, competition, and adaptive evolution, ideas that are central to Darwinian theory and modern evolutionary ecology.

The theory of habitat selection provides valuable insights and support for this discussion. Habitat selection has generally been applied only to motile animals that actively choose among alternative patches through behavioral mechanisms. Recently, Bazzaz (1991) demonstrated the relevance of habitat selection in plant ecology, and Donohue (2003) has proposed novel ideas on the role of phenotypic plasticity as a form of habitat selection. For this discussion, the important result of theoretical studies in this area is that habitat selection will promote specialization to the preferred habitat, especially when there is a positive correlation between habitat preference and performance in the preferred habitat (Holt 1987) and when the selection process itself is cost free (Cohen 1990). The evolution of specialization to a preferred habitat is a combination of stabilizing selection for the niche optimum and directional selection toward lower niche breadth. For plants, setting aside the question of directed dispersal (Bazzaz 1991), the habitat selection process occurs via broad dispersal or prolonged dormancy of propagules, followed by successful germination and

establishment in conditions that fall within the realized niche (in the context of a particular community). If dispersal is random with respect to genotype, the mortality of seeds that do not reach appropriate locations is nonselective. Among those that do germinate, the combination of physiological tolerances and biotic effects on the realized niche would lead to maximal fitness in genotypes that have established in sites close to their optimal conditions. If genotypes were randomly distributed with respect to environment, the differences in selection pressures across microenvironmental gradients would average out and result in stabilizing selection on population mean niche optima. If this argument is correct, the outcome resembles the process of habitat selection, and it guarantees that genotypes will “select” environments in which they exhibit superior performance because the selection process is a direct outcome of competitive performance. A key assumption of this model is that communities are ecologically saturated most of the time (Hubbell 2000). This assumption means that populations will only rarely experience a situation in which they successfully establish in suboptimal conditions (averaged over the entire population) instead of being excluded by a superior competitor. In section 6, I explore several scenarios that may lead to such transient disequilibria between distributions and niche optima.

Is there empirical evidence from the study of selection in natural populations to support the prediction that niche assembly processes promote stabilizing selection? Several types of evidence would be relevant: (1) Is there evidence of stabilizing selection on traits directly related to resource use and performance along niche axes? (2) Is stabilizing selection stronger in the presence of interspecific competitors (i.e., in saturated communities)? (3) Is stabilizing selection stronger when populations are assessed in their native environment? For example, in the first category, Dudley (1996) reported stabilizing selection for leaf size in dry environments and water-use efficiency in wet environments, consistent with predictions regarding optimal trait values. But in a survey of selection studies on plant functional traits, Geber and Griffin (2003) found that the average values of quadratic selection coefficients did not differ from zero, so widespread evidence for stabilizing selection is lacking. Furthermore, a negative coefficient only indicates convex curvature and does not demonstrate that there is a fitness peak within the range of trait values in the population (Mitchell-Olds and Shaw 1987; Travis 1989). I am not aware of any studies in relation to the second question and just one for the third question. Bennington and McGraw (1995) combined phenotypic selection analyses with a reciprocal transplant experiment of *Impatiens capensis*. The one significant result they obtained for stabilizing selection was for flowering time of one population in its home site. This result is in line with the predictions discussed here, but one positive case is insufficient to draw broad inferences. There is a need for more intensive studies of selection on traits directly related to niche occupancy in plant communities, but such studies are extremely challenging because of the large sample sizes required, especially for detection of quadratic coefficients (Mitchell-Olds and Shaw 1987), and the challenges of measuring relevant physiological and growth traits (Ackerly et al. 2000).

5. Phylogenetic Conservatism of Functional Traits and Niche Relations

The development of comparative biology in a rigorous phylogenetic context has renewed focus on patterns of similarity and divergence among related species. As in the study of adaptation, it is critical to distinguish pattern and process in the study of phylogenetic trait conservatism (Burt 2001; Blomberg and Garland 2002). Terms such as constraint and inertia are often invoked to describe patterns of phenotypic similarity on a phylogeny, often implying that nonselective evolutionary processes play an important role in trait evolution. As stabilizing selection provides an adaptive explanation for the same patterns, the observation of trait conservatism on a phylogeny cannot be used to infer the role of selection versus alternative processes (Leroi et al. 1994; Westoby et al. 1995; Blomberg and Garland 2002). While it is beyond the scope of this article to contrast these two perspectives, I hope the discussions so far are sufficient to document the plausibility and evidence in favor of the role of stabilizing selection arising from ecological sorting processes. In this section, I will briefly review four types of evidence that illustrate the prevalence of the pattern of trait conservatism in plant functional evolution: (1) patterns of trait variation on phylogenetic trees; (2) similarities among closely related species in the context of co-occurring species within and across communities; (3) correlations of modern-day ecology with biogeographic or paleoclimatic history; (4) stasis in the fossil record and paleoecological evidence that taxa have occupied similar environments in the present and past, where past environments are reconstructed independently of community composition or physiognomy.

5.1. Phylogenetic Patterns of Functional Trait Evolution

The fact that closely related species share many ecological characteristics is apparent to every naturalist and is a recurrent theme of the *Origin of Species* (Darwin 1859; Ridley 1992). The broad success of morphological systematics is a simple reflection of the fact that trait evolution is relatively slow compared with speciation, so phenotypic similarity, at least for some characters, carries a high degree of phylogenetic signal. The elucidation of molecular phylogenies has corroborated many, though not all, of the results of morphological systematics. Molecular data and improved phylogenetic methods have also improved the resolution of phylogenetic studies, which has greatly enhanced the comparative analysis of functional trait evolution.

In the California flora, the genus *Ceanothus* illustrates patterns of trait differentiation and conservatism in the striking ecological divergence between the two subgenera, *Cerastes* and *Ceanothus* (fig. 2). *Ceanothus* is comprised of ~55 species of woody shrubs predominantly distributed in the fire-prone, mediterranean climate region of California. Most species of subgenus *Ceanothus* are postfire “sprouters,” with relatively high SLA leaves, deep roots, and moderate drought tolerance. Species of *Cerastes* have lost their resprouting capacity and rely on postfire seed germination for regeneration; they have very low SLA leaves, shallow roots, and high drought tolerance (Nobs 1963; Wells 1969; Davis 1989; Davis et al. 1999; Knight and Ackerly 2001a; Bond and Midgley 2003; Ackerly, in

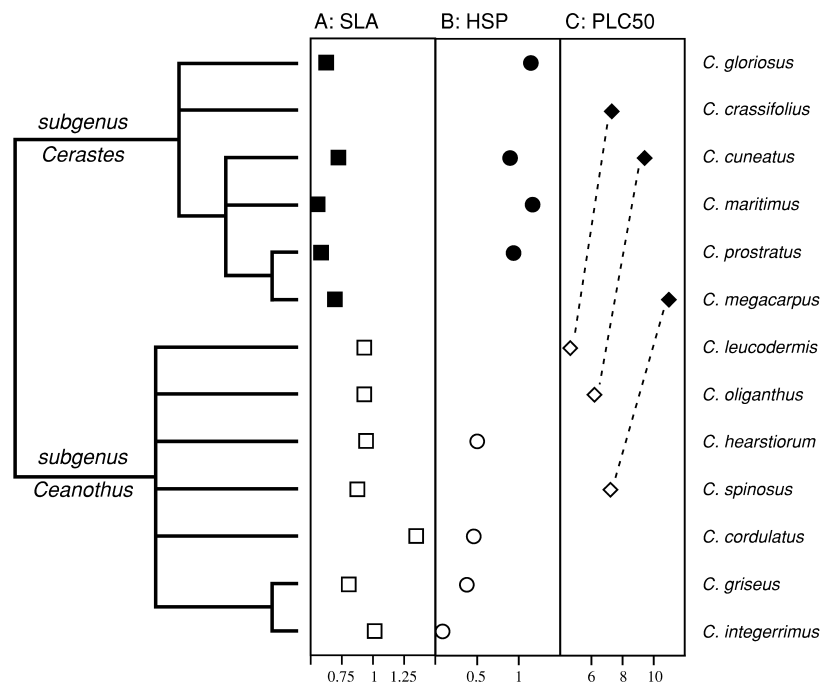


Fig. 2 Phylogeny of a small sample of *Ceanothus* species, illustrating divergence in regeneration strategy and several functional traits. A, Specific leaf area (mm²/mg, log; D. D. Ackerly, unpublished data); lower values indicate thicker and/or denser leaves. B, Expression of low molecular weight heat shock proteins following an experimental heat stress (relative to a standard; Knight and Ackerly 2001a). C, Drought tolerance, measured as the water potential at which stems exhibit 50% loss of hydraulic conductivity due to embolism (PLC50, MPa; Davis et al. 1999). In C, the lines connect sympatric species pairs along an altitudinal gradient.

press). This divergence in a large suite of adaptive traits related to stress tolerance and postfire regeneration dates to a basal split 18–39 million years ago between the subgenera (Hardig et al. 2000). In the subsequent radiation of 25–35 taxa in each group, the species have spread throughout the California Floristic Province and beyond, but these traits have remained remarkably conserved. Many chaparral communities have one or a couple species from each group, exhibiting contrasting strategies and consistent differences in functional traits (fig. 2C) (Davis et al. 1999; Ackerly, in press). The parallel radiations of the two subgenera across California, and their co-occurrence at a community level, are consistent with the predictions presented in this article relating community assembly processes to trait conservatism.

In recent years, a number of comparative methods have been developed to quantify levels of trait conservatism and its distribution at different phylogenetic scales (Ackerly 1999; Morales 2000; Freckleton et al. 2002; Webb et al. 2002; Blomberg et al. 2003). The first quantitative approach to this problem was the use of taxonomic hierarchical ANOVA, which partitions interspecific variance into components among species within genera, among genera within families, etc. For example, studies of seed size in several floras have generally found >60% of variation explained at the family level or above (Lord et al. 1995; Ackerly 1999). However, individual species in many families often exhibit similar extreme low or high values, so this evidence of phylogenetic signal does not represent any absolute constraints (Lord et al. 1995). More recent methods have examined the overall distribution of trait values on a

phylogeny, providing metrics of trait conservatism that may be tested for significance with parametric or randomization models (Cheverud et al. 1985; Legendre et al. 1994; Ackerly and Donoghue 1998; Blomberg et al. 2003).

There have been several applications of these quantitative methods to plant functional traits. For example, Prinzing et al. (2001) examined phylogenetic conservatism in niche preferences for several factors (based on Ellenburg numbers) in >2000 species of central European angiosperms. They found significant conservatism on all niche axes compared to the null hypothesis that traits are randomly distributed across the tips of a phylogeny. The highest levels of conservatism were found for moisture and nutrient preferences, and taxonomic hierarchical ANOVA demonstrated substantial variation at the family level or above for temperature, moisture, soil pH, and soil nitrogen preferences. In the British flora, comparative analysis of ecological traits in >1700 species (Peat and Fitter 1994) revealed high levels of variation at the family level or above for pollination syndromes, breeding systems, life form, mycorrhizal type, genome size, and stomatal distributions; high levels of variation within genera occurred in minimum and maximum height, range size, and altitudinal range limits. The latter is noteworthy as it illustrates low levels of conservatism for a direct measure of climatic distribution limits (the opposite of the predictions discussed here). An analysis of niche differentiation in British meadow communities found cases of significant ecological divergence across the taxonomic spectrum, from congeneric species to the family level and higher (Silverton et al. 2000). In this community context, the results at

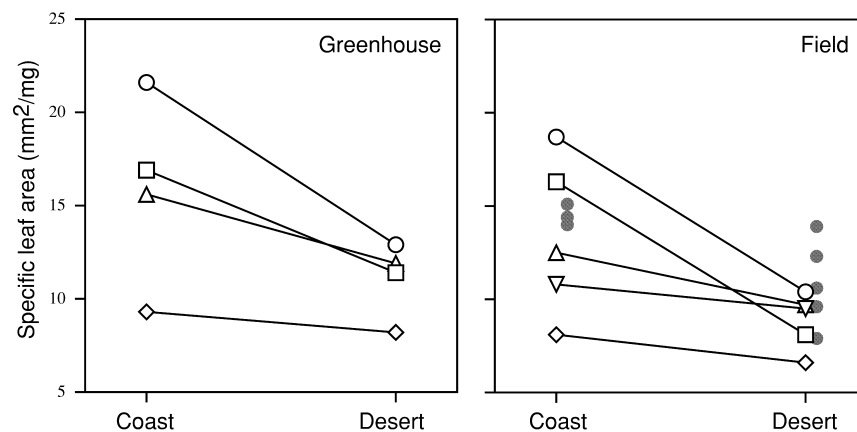


Fig. 3 Specific leaf area of congeneric species pairs from desert and coastal environments of California, raised in a common greenhouse environment (left) and sampled in the field (right). Circles, *Encelia*; squares, *Atriplex*; triangles, *Salvia*; diamonds, *Eriogonum*; inverted triangles, *Isocoma* (field only); shaded circles, other species in the field community. Modified from Knight (2001), with permission.

high taxonomic levels reveal conserved differences in niche preferences in the associated groups of species (Webb et al. 2002). For leaf traits, an analysis of >100 seed plant species from a wide range of habitats also found highly significant conservatism for leaf size and SLA, primarily because of the overall differences between conifers and angiosperms (Ackerly and Reich 1999). In several large clades contributing to the California chaparral (monophyletic groups within the Ericaceae, Rhamnaceae, and Rosaceae), SLA is also significantly conserved (D. D. Ackerly, unpublished data). In an important study illustrating the opposite pattern, *Quercus* species that inhabit various habitats in northern Florida exhibit a high level of evolutionary convergence (across several subgenera) in habitat preference and associated physiological traits; other traits that are conserved within subgenera, such as wood density and disease susceptibility, may play an important role in mediating coexistence (J. Cavender-Bares, unpublished data).

These studies illustrate trait conservatism at a range of phylogenetic scales, and several challenges lie ahead for such studies. First, global data sets need to be compiled for important functional traits reflecting ecological strategies (Westoby et al. 2002). It will then be possible to determine if niche conservatism assessed in local and regional floras reflects global patterns of trait evolution or whether it is a historical contingency of vegetation dynamics and community assembly in particular areas. Second, because of advances in molecular phylogenetics and paleobotany that will provide increasingly accurate absolute ages for plant lineages (Magallón and Sanderson 2001), it will be possible to assess the duration and geologic context of trait conservatism and compare rates of ecological divergence across lineages (Losos and Miles 2002). These developments will provide the tools to test hypotheses regarding the degree of trait conservatism in different traits, lineages, and ecological contexts.

5.2. Closely Related Species in a Community Context

The comparison of closely related species pairs has a long history in comparative ecology (Salisbury 1927) prior to the development of full-fledged comparative methods based on

well-resolved phylogenies (Ackerly 1999). Comparison of ecological traits in related species provides a direct measure of evolutionary divergence or stasis relative to a common ancestor. Replicated comparisons of species pairs with contrasting distributions or life history provide a particularly powerful approach to conduct robust tests of evolutionary hypotheses (Silvertown and Dodd 1996; Cunningham et al. 1999). The feature that has received less attention in such studies is that there are usually significant differences among the species pairs themselves, indicating deeper levels of evolutionary divergence. These differences can be tested statistically as a taxonomic effect orthogonal to the ecological contrast within pairs (see Westoby 1999). Significant differences between the species pairs in such studies indicate a pattern of evolutionary conservatism, and the adaptive differences within each pair occur in the context of these older, conserved divergences. In a community context, this pattern may indicate that species maintain fairly stable relative order in terms of niche relations or functional traits, even if the ecology of the community as a whole exhibits adaptive shifts.

For example, Knight (2001; Knight and Ackerly 2001b) examined photosynthetic thermal tolerance and SLA in four congeneric pairs with species in the Mohave Desert and coastal California. As expected, SLA was higher in the coastal species of each genus, but there were also highly significant differences between genera that were maintained across the climatic gradient (in the field and in common greenhouse conditions) (fig. 3). This pattern indicates that within each community, the various genera occupy similar ecological positions relative to other taxa. Constraints on evolutionary change cannot explain the differences between genera since the species pairs within each genus have diverged considerably. Rather, this pattern is the expected result of evolution in ecologically saturated communities. Lineages will maintain their ecological positions within the community, “hemmed in” by competitors on each side in niche space, even as the functional traits of the entire community shift toward lower or higher values (see Westoby et al. 1998). Assuming that the dynamics of these communities involve individualistic species responses to climatic fluctua-

tions, as in the studies of temperate forests discussed above, this evolutionary process reflects a diffuse process with changing identity of competitors and not the outcome of persistent pairwise species interactions.

Comparisons of disjunct lineages with intercontinental distributions demonstrate that ecological traits can be conserved over tens of millions of years. Analysis of realized climatic niche parameters (see sec. 2) is particularly relevant for the discussion here, as it provides a direct test of evolutionary stasis in climatic tolerances (Peterson et al. 1999). For example, modern *Fagus* spp. of North America and Europe exhibit virtually identical climatic response surfaces in their current distributions (Huntley et al. 1989), and they presumably diverged at least 15 Ma with the disruption of the North Atlantic Land Bridge (Manos and Stanford 2001; Tiffney and Manchester 2001). In a fascinating study, Ricklefs and Latham (1992) found significant correlations of geographic range size between disjunct herbaceous sister taxa in eastern Asia and eastern North America that would have diverged ≥ 10 –30 Ma. They interpret this finding in terms of conservatism of ecological traits that influence distribution patterns, although the underlying functional ecology has not been directly examined. On these time scales, it becomes increasingly difficult to envision the lack of sufficient genetic variation or other nonselective constraints as satisfactory explanations for trait and niche conservatism (Lord et al. 1995; Westoby et al. 1995). Stabilizing selection, promoted by habitat tracking and community assembly dynamics, represents a highly plausible and parsimonious explanation for these patterns.

5.3. Functional Traits and Biogeographic History

Another independent line of evidence for the conservatism of niche relations is the correspondence between contemporary ecological traits and biogeographic history of plant lineages (Williams-Linera 1997). For example, Lechowicz (1984) asked why tree species in a deciduous forest community show a wide range in the time of leaf appearance in spring. This trait is highly conserved, in the sense that congeneric species occupy similar positions in the leafing sequence in temperate forests throughout the Northern Hemisphere. Leafing time is also associated with a suite of hydraulic traits, representing a trade-off between early leafing and cold tolerance versus late leafing and higher hydraulic efficiency. Lechowicz found that the early “leafers” were generally derived from cool temperate lineages (e.g., *Betula*), while late leafers were primarily of tropical lineage origin and had lower cold tolerance and lower resistance to drought-induced embolism (e.g., *Fraxinus*). These historical relations indicate that the intermingling of lineages with diverse biogeographic and climatic histories may be an important determinant of the range of ecological strategies available in the assembly of local communities.

I have conducted a preliminary analysis of functional diversity in the woody flora of coastal California, asking to what extent contemporary variation in climatic distributions, leaf function (SLA), and seed size reflects the historical origins of the respective lineages. Raven and Axelrod (1978) identified five primary floristic groups contributing to the flora of the California Floristic Province: (1) north temperate (the Arcto-Tertiary geoflora), (2) Madro-Tertiary (the subtropical flora

affiliated with Mexico, the southwestern United States, and in some cases the mediterranean region), (3) warm-temperate and desert, (4) South American, and (5) groups centered in the California Floristic Province itself (groups 3–5 are combined here as they exhibited similar patterns in this analysis). With a few exceptions, I have followed Raven and Axelrod’s biogeographic assignments for each genus, although advances in phylogenetics and historical biogeography offer great potential for reevaluation of California flora origins (e.g., Richardson et al. 2000 for *Ceanothus*). To obtain measures of mean climatic niche for precipitation and minimum and maximum temperatures, species distributions, based on overall geographic distribution and elevational range (Hickman 1993), were overlaid on climate maps for mean annual precipitation, minimum January temperatures, and maximum July temperatures (Knight and Ackerly 2001a). Seed sizes were obtained from the Baker Seed Herbarium (Baker 1972; Tweddle et al. 2003) and SLA data from an ongoing study of leaf evolution in California plant lineages (D. D. Ackerly, unpublished data). To provide a regional analysis excluding the mountains and the much wetter north coast, the analysis reported below is based only on species occurring in the central and southern coastal region (Central West and South West zones; Hickman 1993). For each trait, I calculated average values by genus for the species that are present in the coastal regions and compared genus means among floristic groups.

As expected, north-temperate-derived lineages occupy significantly colder ranges within coastal California, reflecting more northerly or higher-elevation distributions compared to the various warm-temperate and subtropical-derived groups (fig. 4). In parallel with these distributions in cooler ranges, specific leaf area was significantly higher in north-temperate lineages, reflecting greater incidence of deciduous taxa. In contrast, seed size was significantly higher in Madroan-derived lineages, consistent with the increase in seed size toward the Tropics (Lord et al. 1997). These patterns illustrate that the biogeographic mix of taxa in a species-rich flora like California may play a significant role in assembling communities with diverse microclimate preferences, growth characteristics, and regeneration strategies. To the extent that diverse biogeographic origins provide a source of ecologically differentiated taxa for the assembly of communities, it will reduce opportunities for local adaptive differentiation and further reinforce niche conservatism.

Advances in phylogenetics, paleoecology, and biogeography will greatly enhance our understanding of the origin and maintenance of functional diversity in different regions of the globe. This knowledge may reveal a greater importance of “top-down” effects on trait evolution and community structure, paralleling evidence for regional and historical effects on species diversity (Ricklefs 1987).

5.4. Similarity of Past and Present Environmental Tolerances

Stasis in morphological traits (leaves, fruits, flowers) is widespread in the fossil record and provides the basis for assigning fossil specimens to extant lineages. It is widely assumed that climatic tolerances are similarly conserved, an underlying assumption of the nearest living relative (NLR) method of re-

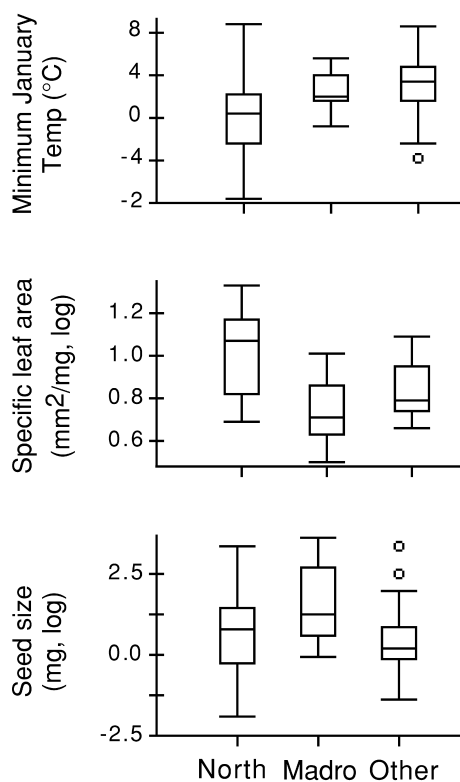


Fig. 4 Realized climatic niche (minimum January temperatures), specific leaf area, and seed size of woody plants of central and southern coastal California as a function of biogeographic origins. Biogeographic assignments primarily based on Raven and Axelrod (1978). North = north temperate Arcto-Tertiary affiliations; Madro = Madro-Tertiary affiliations; Other = groups with temperate desert, South American, and endemic Californian affinities. Values are based on genus means. Boxplots show median (central line), 25th and 75th percentiles (box), and outliers. Differences between groups are highly significant in all three cases (ANOVA, $P \leq 0.001$). Sample sizes for North, Madro, and Other, respectively: climatic niche (70, 19, 69), SLA (13, 11, 20), seed size (49, 16, 53).

constructing ancient climates (sec. 3) (Tiffney and Manchester 2001). However, despite the compelling evidence for rapid migration and fluid community structure, it is important to note that direct evidence for evolutionary conservatism of climatic tolerances is difficult to obtain from the fossil record (Bennett 1997). **The fact that species exhibit individualistic migration patterns does not mean that they are evolutionarily static in terms of niche requirements or related functional traits, as these attributes could also be changing in the course of the migrations.** As noted above (sec. 5.2), the similarity of contemporary climatic preferences in closely related taxa has provided an important test of this assumption for paleoecologists (Huntley 1991). In addition, independent, nonbiotic climate indicators (isotope ratios, etc.) provide confirmation of overall climatic trends inferred from vegetation distributions. However, these approaches do not generally provide precise information on local climatic conditions associated with individual fossil floras. This fact makes it difficult to test directly for stasis or change in climatic tolerances based on the fossil record.

Analysis of leaf physiognomy (Wolfe 1995) provides the primary alternative to the NLR approach, as it relies only on the frequency of various leaf traits in a flora, regardless of taxonomic affinity. I am not aware of any attempts to apply physiognomic analysis to a large set of fossil floras and then to test the inferred climatic tolerances of individual taxa (to maintain statistical independence, the taxa of interest could be removed from the physiognomic data set). As methods of climate reconstruction are refined further, there will be great potential to test hypotheses of stasis and change in climatic tolerances and ecological relations of plant lineages.

In summary, there is widespread evidence of phylogenetic conservatism in ecologically important traits. In recent years, the question of conservatism has been cast primarily in terms of the distributions of traits on phylogenetic trees. The discussion here emphasizes that this is just one of several lines of evidence. Important directions for future research will include the synthesis of paleobotanical and phylogenetic evidence on trait evolution, an explicit focus on rates of trait evolution based on more accurate dating of phylogenetic divergences, and the analysis of trait variation in the context of both phylogeny and community structure.

6. When and Where Does Adaptive Evolution Occur?

The discussions above argue for the importance of community assembly and migration as ecological processes that maintain the “fit” between organismal tolerances and environmental conditions. In terms of niche theory, this fit is reflected in the degree of correspondence between a species’ physiological optima on various abiotic gradients and the position it occupies in multidimensional niche space. Comparative studies provide widespread support for the maintenance of ecological character over millions of years. This stasis can be explained in part by community assembly and migration, which will promote evolutionary conservatism in niche relations and associated functional traits. However, this thesis seems at odds with extensive evidence of natural selection on functional traits and local adaptation of populations and closely related species. This seeming contradiction can be resolved by arguing that local adaptation occurs within narrow bounds, in the context of deeper levels of conservatism among more distantly related lineages. What is needed, though, is a conceptual framework that encompasses local and regional assembly processes in relation to adaptive evolutionary change under directional selection. In this section, I examine three distinct scenarios for adaptive evolution where species, populations, or individual genotypes are expected to encounter a mismatch between organismal adaptations (i.e., current physiological optima) and abiotic conditions. I do not address coevolutionary dynamics between interacting species or the role of population genetic processes (gene flow, drift, mutation, and recombination) that can prevent species from reaching adaptive peaks.

6.1. The Hutchinsonian Niche Space and the Realized Environment

The framework for the models presented here is the distribution of species in the Hutchinsonian n -dimensional niche space (Hutchinson 1957). In Hutchinsonian terms, the distri-

bution of a species is explained by its physiological tolerances (fundamental niche) and its performance in the presence of competitors and other biotic interactions (the realized niche). However, a subtle assumption implicit in discussions of Hutchinsonian niche theory is that all combinations of the relevant environmental factors actually exist somewhere in the landscape, such that the fundamental and realized niche relations are sufficient to predict species distribution and community structure. This assumption is not well founded in the real world. The interactions of topography, geography, and climate create limited combinations of environmental factors at all scales of analysis. Physiological ecologists recognize this problem in the analysis of spatial and temporal “congruence” of multiple resources necessary for plant growth (Bazzaz 1996). It is also implicit in theories of diversity, especially for vertebrate communities, that focus on the range of habitat or food types available in the environment. Jackson and Overpeck (2000) have formalized this problem by introducing the concept of the “realized environment,” defined as the combinations of different environmental factors that are realized in a given landscape at a given point in time. For example, plots of summer versus winter temperature at a continental scale reveal a broad scatter of points with a weak positive correlation; certain combinations of conditions do not exist anywhere (e.g., summer temperatures $>25^{\circ}\text{C}$ and winter temperatures $<-20^{\circ}\text{C}$; fig. 1 in Jackson and Overpeck 2000). Species distributions and community structure must be understood in terms of species’ environmental tolerances with respect to relevant environmental axes and the joint distribution of the environmental factors themselves. Jackson and Overpeck define the “potential niche” as the intersection of the realized niche with the realized environment to describe the set of actual habitats that could be occupied by a species in a given landscape. This conceptual framework clearly shows how species that are limited by different environmental factors (e.g., drought vs. freezing) may exhibit contrasting responses to the same set of climate changes (figs. 4–6 in Jackson and Overpeck 2000).

In the following three sections, I apply the concept of the realized environment to the question of adaptive evolution. I present three generalized scenarios in which the interaction of community assembly and migration will result in populations occupying habitats that are suboptimal with respect to their environmental tolerances. This “mismatch” between organism and environment creates the necessary pressure for directional selection that will promote adaptive evolutionary change.

6.2. Evolution on “Environmental” Islands

The invasion of new, unoccupied habitats is a well-recognized scenario for adaptive evolution. This is most famously documented on volcanic island chains (e.g., Hawaii, Galápagos), where the absence of competitors and herbivores, heterogeneous topography and substrates, and intrinsic barriers to dispersal promote both adaptive diversification and speciation (Carlquist 1974). In many cases, the initial colonists on islands are herbaceous, weedy plants that are well suited for long-distance dispersal and establishment in new habitats (Givnish 1998). Isolated habitats on continents may also be viewed as climatic or habitat islands (e.g., mountaintops, ser-

pentine soils) that impose strong selective pressures on colonizing populations. The importance of these geographically isolated habitats is that extreme dispersal limitation promotes adaptation and diversification of the successful colonists, providing natural experiments in evolution.

Here, I want to introduce a different kind of island, based on the distribution of realized environments, that has important implications for patterns of functional evolution. I define an “environmental” island as a habitat that is discontinuous in the realized environmental space from other habitats in the landscape (fig. 5). Environmental isolation in this sense will influence the functional attributes and environmental tolerances of colonizers and subsequent pressures and opportunities for adaptive evolution. Environmental islands may or may not be geographically isolated; the primary trait required for initial colonization of an environmental island is a broad fundamental niche in the appropriate dimensions to allow initial establishment and regeneration. In the absence of competitive exclusion, opportunities for adaptive evolution may follow for populations that can persist in these novel conditions.

In many cases, geographic islands (e.g., Hawaii) will be environmental islands as well. The bare (and often volcanic) soil and equable oceanic climates are unlike the conditions found on continental areas that would serve as sources for colonizers (fig. 5A). In terms of functional evolution, this isolation in habitat space means that potential colonizers from nearby continental areas are unlikely to possess appropriate specializations for the combination of environmental conditions on the environmental island. The fundamental niche of potential colonizers will have to encompass the island conditions, but the lack of competitors and herbivores would allow successful establishment even if conditions are far from the species’ physiological optima. As a result, the new population would experience strong selection for shifts in niche optima along one or more axes, promoting rapid adaptive evolution in such populations. One consequence of this scenario is that the direction of evolutionary change in environmental tolerances from the source population to the evolving colonizing population may be quite unpredictable; the primary factor influencing arrival would be high dispersal ability, which may be correlated with other life history traits of colonizing species but not with particular physiological tolerances. The contingencies of dispersal may influence the order of arrival and the source area of colonizers more than their environmental tolerances or functional ecology (fig. 5A, species A–C).

In continental landscapes, the best examples of environmental islands are extreme edaphic habitats (serpentine soils, heavy metal mine tailings, acid bogs, etc.). Colonizing populations from adjacent habitats would exhibit appropriate climatic adaptations, but they would require large shifts in edaphic tolerances (fig. 5B, species A). Alternatively, long-distance colonizers from other patches with similar edaphic conditions would be under selection for changes in climatic tolerances (fig. 5B, species B). Independent evolution of zinc-tolerant populations below electricity pylons illustrates the interaction of small-scale dispersal limitation and strong natural selection, as tolerance evolved repeatedly from adjacent non-tolerant populations (rather than evolving once and then dispersing between the discontinuous patches of extreme conditions) (Al-Hiyaly et al. 1993).

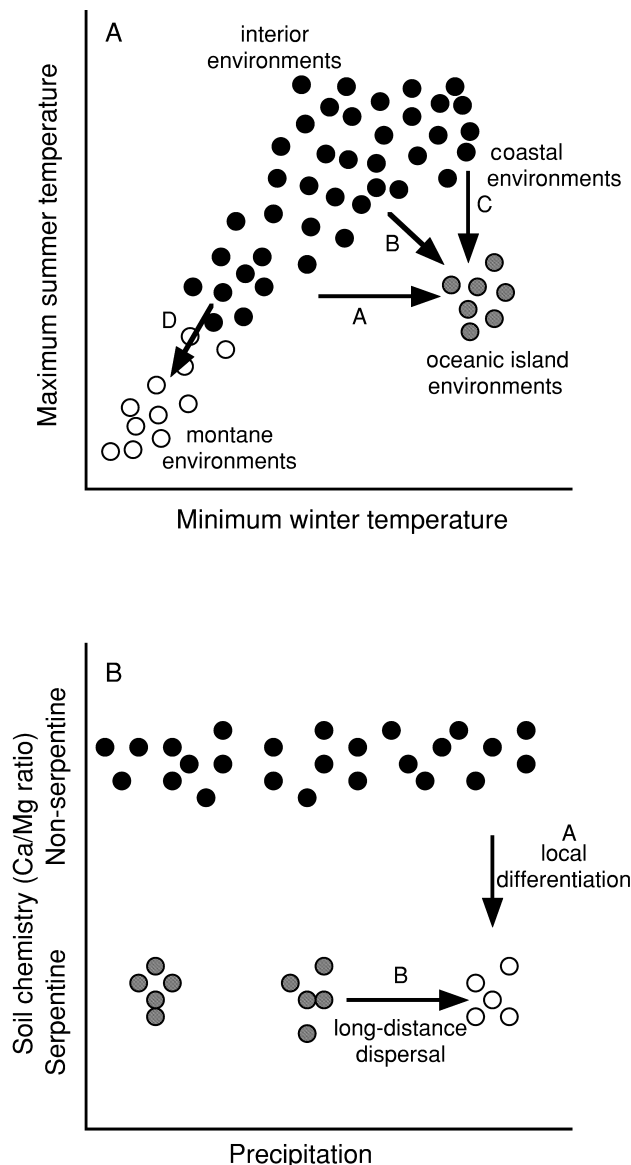


Fig. 5 A, Schematic diagram of winter versus summer temperatures in coastal California. Each point shows climatic conditions in a local area, and species ranges would encompass varying portions of the realized environments. “Environmental” islands are defined as areas that are discontinuous in environmental space (here shown as the conditions on oceanic islands that have cool summers and warm winters). Colonizers of these island environments could arrive from locations with different combinations of summer and winter temperatures (species A–C), depending on contingencies of dispersal, but none will be closely matched in environmental tolerances on both axes. Mountaintops, which can be considered climatic islands, are not isolated in the environmental space, so colonizers can arrive from closely adjacent conditions at lower latitudes (species D). B, Hypothetical edaphic islands along a precipitation gradient that are discontinuous in the environmental space, although they are contiguous in physical space with surrounding areas of similar precipitation. Colonization of a new area (open circles) requires either an adaptive shift in local populations (species A) or long-distance dispersal of serpentine ecotypes with an adaptive shift in tolerance along the precipitation gradient (species B).

Many island-like habitats on continents will not be discontinuous in environmental space and so do not represent environmental islands. For example, the climatic conditions on mountaintops represent extreme conditions (low temperatures, exposure, etc.), but they are contiguous in both physical and environmental space with adjacent subalpine conditions. Colonizers of a new alpine zone (e.g., during a cooling trend) could evolve from subalpine taxa by small gradual shifts in cold tolerance (fig. 4A, species D). This process is distinct from the larger adaptive shifts required to colonize and adapt to an uninhabited, environmental island and may be an example of “trailing-edge” evolution covered in the next section. The analysis of realized environmental distributions with respect to climatic and edaphic factors will identify habitats that represent environmental islands, in the sense discussed here, and provide a valuable basis for studies of adaptive shifts in environmental tolerance and results for community assembly.

6.3. Climate Change, Migration, and Adaptation: The “Trailing-Edge” Hypothesis of Adaptive Evolution

In saturated communities where conditions are contiguous in environmental space, the most obvious factor that will lead to an adaptive mismatch between organisms and environment is a temporally changing environment, causing conditions to shift within a population’s current range. Climate change is ubiquitous in earth history, and environmental variability at all scales should be given a central role in ecological and evolutionary theory (Bennett 1997). A population may exhibit one or more of several responses to changing environments (Jackson and Overpeck 2000): (1) local shifts in microhabitat or altitudinal distribution; (2) large-scale changes in geographic distribution, entailing both range expansions and widespread extirpation in the former range; (3) adaptive evolution of the niche in response to the new conditions; (4) extinction.

These four possible responses suggest that there will be a negative correlation between dispersal ability and adaptive change (at least among the species that survive an episode of climate change); species with high dispersal potential can migrate rapidly with little adaptive change, while poor dispersers will either adapt or go extinct. However, this conclusion does not fully account for the interactions among competing species in a community and the consequences for survival and adaptive evolution. Incorporating this community perspective leads to a novel view of adaptive evolution in response to climate change.

Consider a one-dimensional spatial landscape with a monotonic gradient of some environmental factor (e.g., the temperature gradient with latitude or altitude) (fig. 6). If we assume that the current set of species in the landscape are close to equilibrium in terms of their tolerances along this gradient, there would be a classic Gleasonian pattern of species replacement reflecting individual environmental optima and niche breadths. Now, if climate changes at a modest rate, species will be able to migrate and track conditions that match their realized niche. The range of each species shifts by enhanced population growth in locations at the leading edge and reduced performance and negative population growth at the trailing edge. As migration proceeds, the trailing edge occupies the location that was previously the center of the population’s

distribution along this niche axis, although conditions would now be increasingly suboptimal for this species (Hewitt 2000). These range shifts reflect the outcome of competitive interactions (assuming saturated communities) as individuals at one edge of their range exhibit enhanced performance under the changing conditions and outcompete previously dominant species, which now find themselves in suboptimal conditions. Populations may persist initially due to the advantages of prior occupancy. However, they are not likely to adapt genetically fast enough to resist the eventual invasion of competitors from adjacent positions, especially since the competitors have the advantage of many generations of past selection under the appropriate conditions. These are rather sweeping and simplistic assumptions, but (as already discussed) the history of rapid migration supports the view that species replacement usually outpaces local adaptation.

On this one-dimensional gradient, where would adaptive evolution occur? It is tempting to focus on the leading edge of the moving vegetation, especially in revegetation following glaciation, as these populations encounter open habitat and opportunities for rapid population expansion. However, in the simple model of a single-factor gradient, the leading edge will either be the site of extinction (e.g., alpine species “pushed” off a mountain top by warming; species *D* in fig. 6A) or of a range shift as populations track favored conditions (species *C*). In contrast, the potential for adaptation will arise where there is no “preadapted” population or species arriving in a location to compete with the resident populations, allowing the latter to persist under suboptimal conditions. This situation will occur in the trailing-edge populations of the species at the warm end of the gradient (in this example), where novel conditions appear that had no prior analogue along this gradient and a dispersal barrier limits colonization by populations with appropriate adaptations. During warming trends, these conditions would occur on the equatorial edges of continents (e.g., the Mediterranean coast of Europe) or possibly on the polar flanks of east-west oriented mountain ranges (e.g., the north slope of the Alps). Rising sea levels during warming periods will enhance intercontinental dispersal barriers, reinforcing this process (Vrba 1997). During periods of cooling, analogous situations would arise on mountaintops and at high latitudes (unless they are glaciated, preventing all vegetation growth). Assuming effective dispersal barriers, these pockets of new conditions are physically discontinuous from comparable environments that could serve as sources of appropriately adapted species. They are not, however, environmental islands, as defined above (sec. 6.2), and they would already be occupied by preexisting vegetation. Thus, despite the deteriorating environment, the resident populations at the trailing edge of a species could persist from lack of competition (fig. 5A, population *A'*). The leading-edge populations in these species could also expand their range to track preferred climatic conditions (population *A*). This would lead to expansion in geographic and environmental range for this species.

Several evolutionary scenarios could follow in this situation. If there was high gene flow among populations, there would be selection for increased niche breadth, possibly by enhanced physiological plasticity in underlying climatic tolerances. Alternatively, restricted gene flow could lead to ecotypic differentiation in environmental tolerances, from divergent selection

across the species' range. If significant barriers to gene flow are present, speciation is conceivable, but on the time scales required for speciation continued climate change could overwhelm incipient differentiation. Of particular interest is the possibility that environmental deterioration leads to declining population size in the trailing-edge populations and to risk of extinction. In time, these populations might be rescued from their demographic fate by adaptive evolution. By modeling the demography and population genetics together, Gomulkiewicz and Holt (1995) have shown that the probability of survival by adaptation depends on the degree of initial maladaptation and (unless maladaptation is very high) the initial population size. In addition, these maladapted populations could become demographic sinks maintained by immigration from source populations closer to the species' environmental optimum. The immigrants would carry maladapted alleles from the source population, possibly diluting the results of selection for local adaptation. However, if the absolute fitness of the immigrant alleles is <1 , they will not reverse the demographic decline in the population. In this case, the immigrants may serve to keep the population alive longer, thus providing time for a locally adapted mutation with absolute fitness >1 to arise. Such a mutation could then lead to population growth and a resulting reduction in the immigration rate and the demographic and genetic effects of immigrant individuals and alleles (Holt and Gomulkiewicz 1997; Gomulkiewicz et al. 1999).

It is important to note that the dispersal capability, or lack of it, in this “last” species on the gradient is not the factor that promotes adaptive evolution; rather, it is the lack of competitors dispersing into the habitat as the climate changes. An analogous situation could arise in the middle of the gradient if one species had extremely poor dispersal. Again, assuming that neighboring species with appropriate climatic optima successfully invade and outcompete resident populations, the most likely fate of a poor disperser would be extinction rather than adaptation (fig. 6B, species *B*). This species' failure to migrate would then promote adaptive response to climate in the trailing-edge populations of the adjacent species along the gradient (fig. 6B, species *C*). By extension, if all species have poor dispersal or the climate change is very rapid, then adaptive responses may be more prevalent across the entire community (unless climate change exceeds absolute physiological tolerances, leading to widespread vegetation collapse). If this general line of argument is correct, then the adaptive response of each species is a function of dispersal ability of competitors, not its own dispersal characteristics. This may be termed the “trailing-edge hypothesis” of adaptive evolution and provides the second scenario of adaptive evolution with respect to the realized environment.

6.4. Adaptation in Multiple Niche Dimensions: The “Relative Niche-Breadth” Hypothesis of Adaptive Evolution

If just one environmental axis is considered, the only new conditions that arise under climate change are at the extreme edge of the gradient (e.g., at low latitude or altitude in a warming climate). While a useful starting point, this scenario is clearly insufficient to capture the complexities of plant responses to climate change. Most importantly, climatic factors

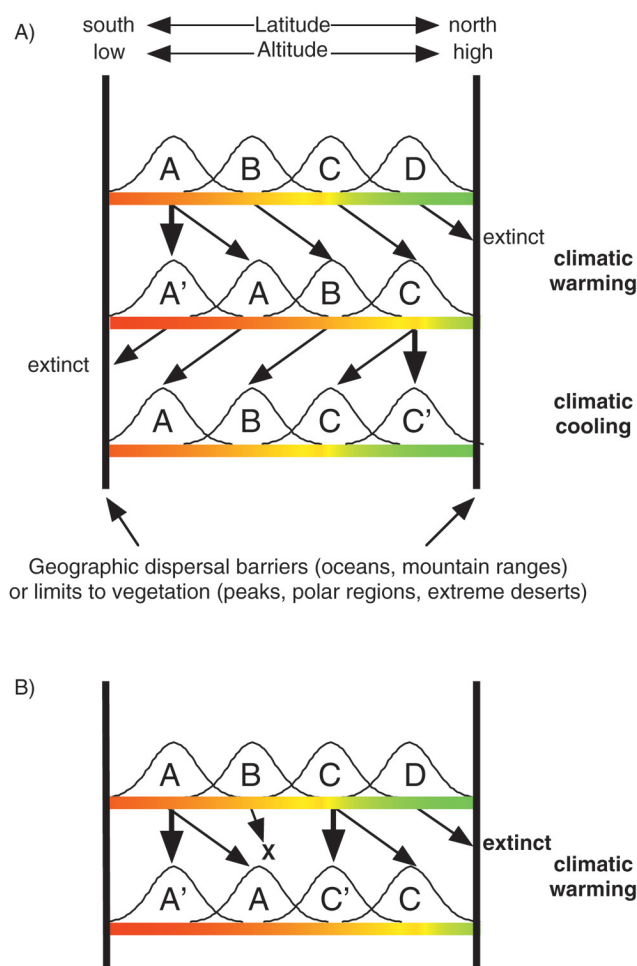


Fig. 6 Diagram indicating hypothesized responses of species migrating along a unidimensional niche axis in response to climate change. A, Potential for adaptive divergence in the trailing-edge populations of species A, which does not face competition from species dispersing from warmer environments. B, Potential for adaptive evolution in trailing-edge populations of species C in the center of the gradient, due to dispersal limitation of an adjacent competitor. See discussion in text.

do not all change in concert, so it is impossible for a species to “track” the environment simultaneously on all axes (Bennett 1997; Jackson and Overpeck 2000). Paleoecologists have emphasized the importance of shifts in multiple environmental factors as drivers of species distributions and community change. The appearance in the fossil record of “no-analogue” communities, which have combinations of species no longer found together today, reflects the distribution of no-analogue climatic conditions (Williams et al. 2001).

Jackson and Overpeck (2000) have argued that changes in the realized environment in a multidimensional niche space can have surprising and nonintuitive results for community responses to climate change. In one striking example, they demonstrate that the relative position of species along a gradient can actually be reversed if species distributions are limited by different factors. In this section, I extend Jackson and Over-

peck’s model to explore the consequences of multidimensional gradients and limitations in realized environments for predictions regarding adaptive evolution.

The hypothesized interactions of niche breadth, range shifts, and adaptive evolution are illustrated in figure 7. Consider a landscape with strong spatial gradients in temperature and precipitation and therefore a positive correlation in the distribution of realized environmental conditions on these two axes (temperature and precipitation are used for illustration only). Assume that species *S* occurring in this landscape has an asymmetrical fundamental niche, with narrower tolerances along the temperature axis compared to the precipitation axis. The range of conditions observed across the landscape can be used as a standard to scale each axis, since they are measured in different units. The potential niche, which describes the actual distribution of this species in the environmental space, is defined by the intersection of the realized environment and the fundamental niche (fig. 7A; see fig. 2 in Jackson and Overpeck 2000).

In the first scenario, assume that there is a uniform increase in precipitation across the entire landscape and no increase in temperature. As a result, the distribution of realized environmental states shifts to the right (fig. 7B). The response of *S* can be considered, somewhat artificially, in two steps: first, a potential shift in geographic distribution to track shifting conditions, and second, a possible adaptive shift in the fundamental niche. In this case, the increase in precipitation across the range of this species will not cause a shift in geographic distribution because its range is more strongly controlled by its narrow temperature tolerance. As a result, the potential niche of the species shifts to a higher rainfall regime, reflecting the increase in precipitation *in situ* across the current range. This shift creates the potential for adaptive evolution. The narrow temperature tolerances constrain the species’ distribution to suboptimal precipitation levels, favoring an evolutionary response in the fundamental niche toward a higher precipitation optimum (fig. 7C). Thus, an increase in rainfall does not result in a range shift, but it does create the potential for adaptive evolution due to disequilibrium between the species’ ancestral precipitation optimum and the new conditions within its range.

The second scenario involves an increase in temperature. In this case, the species’ narrow temperature tolerance would result in a geographic range shift because conditions in the ancestral range have deteriorated significantly. This shift in distribution (poleward or upward in elevation) would move the species to areas of lower rainfall; as in the previous scenario, this shift is tolerated due to the greater niche breadth along the precipitation axis (fig. 7D). As a result, adaptive evolution would again favor a shift in the precipitation optimum, this time toward a lower value compared to the ancestral state (fig. 7E). Interestingly, changes in the two environmental factors have contrasting results in terms of range shifts (in one case the species stays in place, and in the other it shifts in concert with climate), but in both cases the potential for adaptive evolution is observed for the same factor, the one for which the species has a broader fundamental niche (precipitation in this hypothetical example). Again, it is important to note that the relative scaling of different environmental factors is somewhat arbitrary, but this argument holds when the axes are com-

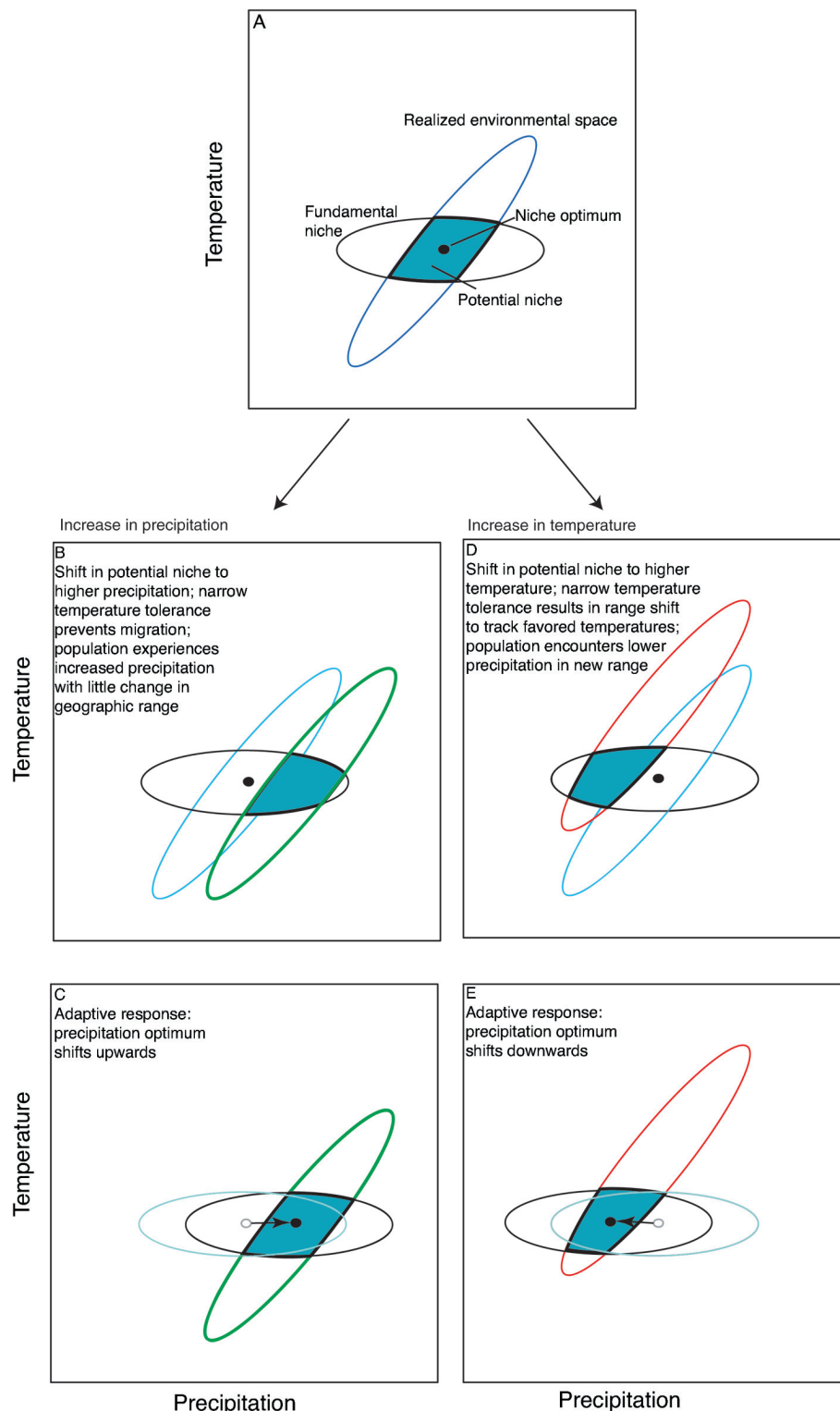


Fig. 7 Diagram indicating responses of a species with asymmetric niche breadths to changing environments. *A*, Potential niche of the species initially, based on the intersection of its fundamental niche with the realized environmental states along hypothetical temperature and precipitation gradients. *B*, Change in potential niche due to increased precipitation; species does not exhibit geographic range shift because its distribution is constrained by narrow temperature tolerance. *C*, The increase in rainfall in the species range results in selection for increases in precipitation optimum of fundamental niche. *D*, From the same starting point (*A*), an increase in temperature results in a geographic range shift because distribution is primarily influenced by the narrow temperature tolerance. This causes the species to move to drier locations and effectively experience the climate change as a decrease in precipitation. *E*, The result is selection for reduced precipitation optimum of the fundamental niche. See additional discussion in the text.

pressed or expanded relative to each other, as the scaling influences the shape of both the fundamental niche and the realized environmental distributions.

There are two aspects of this graphical model that may seem particularly unrealistic. First, only one species from the community is considered, and the focus is on the fundamental niche, with no explicit consideration of biotic interactions. I predict that the results of this model would hold in a more complex model involving multiple species, overlapping niche distributions, and simultaneous responses to climate change in all species. We are currently developing a model to explore this hypothesis (Schwilk and Ackerly 2003). The second, and possibly more problematic, aspect is that I consider only shifts in the optimum of the fundamental niche and not in the niche breadths themselves (see sec. 6.3 on the trailing edge). It is certainly plausible that the adaptive response to these climate changes would involve increases in niche breadth to ameliorate the effect of occupying suboptimal environments rather than shifting the optimum. The evolution of niche breadth is a complex problem dependent on gene flow, the scale of environmental heterogeneity, and possible trade-offs between niche breadth and maximum performance, and it will be important to consider this in future discussions of these hypotheses.

The important conclusion from this analysis is that the underlying cause of the adaptive responses is the relative niche breadth along the two axes, regardless of which environmental factor actually changes. Because of its migratory response, the species in this example would experience an increase in temperature as a shift toward lower rainfall environments. The implication is that there will be more adaptive evolution for niche optima along environmental axes with greater niche breadths, unless the niche breadth is so high that populations experience little negative impact from shifting their distributions. To the extent that plasticity in morphology or physiology contributes to niche breadth, this scenario is similar to the Baldwin Effect, in which a plastic response to environmental change facilitates survival and the potential for subsequent adaptive specialization (Simpson 1953). This result runs counter to the intuition that a broad niche will facilitate persistence in a variable environment and thus reduce selection pressure. The positive relationship proposed here between plasticity and adaptive evolution emerges from two aspects of this scenario. First, only a limited set of environmental conditions exists, so species cannot track their preferred environment simultaneously in multiple dimensions. Second, effective dispersal will cause species to track preferred conditions for factors with narrow tolerances, counteracting the potential for stronger selection along these specialized axes. This process may be termed the “relative niche breadth” hypothesis for adaptive evolution.

6.5. Vegetation History of Western North America

The scenarios discussed in sections 6.2–6.4 may provide a useful framework for considering the history of vegetation change and functional evolution in the American West (Graham 1999 for a detailed review of climate and vegetation history). Eocene climate (>34 Ma) was equable over most of the continent, and a long-term cooling and drying trend started around the Eocene-Oligocene transition (34–35 Ma). The rise

of the Rockies and later the Sierra Nevada, combined with cooling, would have created novel high mountain environments. As vegetation migrated downward on the rising mountain slopes, these new conditions would correspond to trailing-edge environments (fig. 5), and new alpine-adapted populations could have arisen from lower-elevation ancestral populations. Orogeny also created rain shadows in the plains and the Basin and Range. This increase in aridity, relative to temperature regimes, would correspond to the model of shifting realized environments (fig. 7), and adaptive responses may have been driven by relative niche breadths of species in the regional flora. Species with broad tolerance on precipitation gradients, but narrow temperature responses, would have successfully persisted or invaded the rain shadow areas and then undergone further evolution for drought tolerance (Axelrod 1967). Drought tolerant lineages such as *Cercocarpus* and relatives (Rosaceae; Potter et al. 2002) and the arbutoid Ericaceae (*Arbutus*, *Arctostaphylos*; Hileman et al. 2001) may have originated in the West during this period of aridification, and may be viewed in this context.

The origin of the mediterranean-type climate and flora of California is particularly interesting. Summer rain apparently prevailed throughout the West through the Late Pliocene (<3 Ma), when the rise of the California Coast Range, shifts in ocean circulation, and glacial climatic cycles led to summer drought in coastal areas (Axelrod 1973). At this time, a taxonomically and ecologically diverse flora inhabited the region, but taxa requiring summer rain were eliminated by these changes. The species that persisted presumably possessed broad tolerances for growth under summer drought, even before these environments appeared. The relevant characteristics (sclerophyllous evergreen leaves, drought-tolerant xylem, and perhaps adaptations for postfire regeneration) may have arisen in semiarid winter rain environments (Valiente-Banuet et al. 1998), or exposed and/or shallow soil habitats (Axelrod 1972), and then facilitated population expansion under summer drought. Their persistence would then set the stage for further evolutionary modifications adapting to the new climate (Axelrod 1989). For example, summer drought and resulting vapor pressure deficits lead to increased transpirational demands and a potential reduction in water-use efficiency. Comparisons of gas-exchange characteristics in chaparral-type communities of Mexico and California indicate that leaf-specific hydraulic conductivity is higher in the mediterranean-type climate of California, as predicted to meet this increased demand (Bhaskar et al. 2003; see Valiente-Banuet et al. 1998). In the chaparral, the most dramatic instance of adaptive change in functional morphology is the evolution of needle-like leaves in the dominant genus *Adenostoma* (Rosaceae). Molecular evidence links this genus to the American desert shrub *Chamaebatiaria* and an Asian forest tree, *Sorbaria* (Potter et al. 2002), indicating a dramatic evolutionary reduction in leaf size and SLA (D. D. Ackerly, unpublished data). *Adenostoma fasciculatum* (chamise) currently forms virtually monospecific stands over hundreds of square kilometers and is dominant throughout the chaparral region of California. However, there is virtually no fossil record of the genus (Axelrod 1973; Graham 1999) and no evidence regarding the environmental context of these dramatic evolutionary changes in leaf morphology. The mediterranean-type climate may be a highly transient feature of in-

terglacial episodes, and the history of lineage diversification, functional evolution, and Quaternary vegetation change in the California flora remain very poorly understood.

7. Conclusions

The discussions in this article draw on a broad range of conceptual and empirical topics, an endeavor that has led me to gloss over various problems that are critically important for a full elaboration of the overall thesis. For purposes of discussion, I have assumed that dispersal and fecundity limitation are not significant factors in community assembly, an assumption that is only workable at certain temporal and spatial scales. I have focused on plant strategies and niche-assembly processes related to abiotic environmental axes, and the dynamics of evolution in relation to biotic factors may be quite different. I have given only passing consideration to the role of plasticity in relation to environmental variation and niche breadth, a key problem to understand the evolution of developmentally flexible functional traits. And I have ignored the vital question of niche construction, the modification of the environment by the organisms that occupy it, and the consequences for community ecology and evolution (Odling-Smee et al. 1996). The purpose of this simplified view is to provide a starting point for synthesis of ecological sorting processes and adaptive evolution in relation to plant function and community structure. On the one hand, community ecologists (and to some extent paleoecologists) have treated species as fixed entities so that they can more easily understand the dynamics of community organization and vegetation history. Hubbell's (2000) neutral model demonstrates that many features of community structure can be explained without even invoking ecological differences among species; synthesizing this view with the actual diversity of function and life history is an important task. In contrast, evolutionary ecologists have focused on adaptation and convergence to explain the "fit" of organisms and the environment, often invoking the current adaptive role of functional traits to infer their selective history. The latter point has been extensively critiqued and debated in discussions of the meaning of adaptation and the nature of constraints on adaptive evolution (Gould and Vrba 1982; McKittrick 1993; Reeve and Sherman 1993).

The synthesis of ecological sorting processes and adaptive evolution, as I have presented it in this article, leads to a focus on niche conservatism and stabilizing selection as predominant features of evolution. In fact, niche conservatism is one of the processes championed by the proponents of stasis in the punctuated evolution debate (Gould 2002). However, the importance of niche conservatism needs to be reconciled with widespread evidence of local adaptation and patterns of evolutionary divergence. In this context, I have presented a preliminary conceptual scheme that identifies distinct scenarios in which populations may successfully establish under sub-optimal conditions, thereby promoting adaptive evolutionary shifts of environmental tolerances and niche parameters. These scenarios emerge from an explicit consideration of the "realized environment," the combinations of environmental factors that exist at a given point in time, and the way in which changes in the realized environment may generate opportunities for adaptive evolution. These scenarios provide a set of predictions about the situations in which adaptive evolution is predicted to occur, the predictability of the trait changes that may occur, and the relationship between niche breadth and the evolution of environmental tolerances. I hope that future studies integrating biogeography, paleoecology, functional ecology, and phenotypic evolution will undertake tests of these predictions in an effort to refine or refute the underlying model.

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