Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages

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One of the most important floristic sorting periods to affect modern plant communities occurred during the shift from the wet Tertiary period to the unusually dry Quaternary, when most global deserts developed. During this time, a wave of new plant species emerged, presumably in response to the new climate. Interestingly, most Tertiary species that have been tracked through the fossil record did not disappear but remained relatively abundant despite the development of a much more unfavorable climate for species adapted to moist conditions. Here we find, by integrating paleobotanical, ecological, and phylogenetic analyses, that a large number of ancient Tertiary species in Mediterranean-climate ecosystems appear to have been preserved by the facilitative or "nurse" effects of modern Quaternary species. Our results indicate that these interdependent relationships among plants have played a central role in the preservation of the global biodiversity and provided a mechanism for stabilizing selection and the conservation of ecological traits over evolutionary time scales.

Mediterranean-type ecosystems | Mexical shrubland | phylogenetic niche conservatism | plant facilitation | stabilizing selection

The evolutionary processes that drive speciation and create biological diversity are central to the natural sciences, but we know little regarding the historical ecological processes that have eliminated species from communities or allowed them to persist (1). Current plant communities are the product of historical sorting processes and, therefore, include mixtures of floristic elements originating in different geological times and, presumably, under different ecological scenarios (2). Many extant plant species are millions of years old (3) and, therefore, have persisted through dramatic changes in global climate. Biogeographic and paleontological evidence indicates that communities are derived from species that have originated in different geological times and places, and that these taxa have been mixed and culled independently of each other through various sorting processes (2, 3). The perception that interdependent processes among plant species are insignificant over evolutionary time frames has been central to the idea that communities are "merely a coincidence" (4) and the development of neutral model theory on biodiversity (5). Therefore, with few exceptions (6, 7), plant communities are not thought to possess stable properties determined by plant–plant interactions.

In contrast to existing theory, our observations of ecological relationships among species in semiarid communities around the world suggest that powerful facilitative ecological interactions among plant species have been a crucial component of the historical and sorting processes responsible for the composition and diversity of contemporary plant communities. Facilitative interactions appear to have been particularly important during the shift from mesic Tertiary period to the unusually dry Quaternary when global deserts developed. Desertification provided a strong stimulus for the emergence of new taxa (8), but many Tertiary species, adapted to moist conditions, did not go extinct despite the development of a progressively drier climate but remained relatively abundant (3, 9). We quantitatively analyzed the relationship between the evolutionary histories (the periods when particular taxa evolved) of taxa in Mediterranean-climate plant communities and how these same taxa interact with other species during recruitment. Specifically, we compared the importance of facilitative interactions for recruitment between contemporary Tertiary and Quaternary taxa in Mediterranean-type communities around the world by integrating biogeographic, paleobotanical, and ecological literature. We asked whether recent species, those that evolved during the xeric Quaternary and presumed to possess drought-tolerant traits, facilitate ancient species that evolved during the mesic Tertiary and are presumed to be less drought-tolerant.

The ecology and evolution of Mediterranean-type ecosystems are well studied (2, 3, 9–13), and although these climatic regions occupy <5% of the Earth's surface, they harbor almost 20% of the known vascular plant species diversity on Earth. As in other ecosystems, Mediterranean-climate communities are the result of historical effects and sorting processes occurring in different geological times and different ecological scenarios (3, 13).

Many extant taxa in Mediterranean climates originated in the Tertiary [65 to 2 million years (Myr) B.P.] (9, 10) and now are mixed with recent taxa that evolved at the end of Tertiary and beginning of the Quaternary (2 Myr B.P., post-Pliocene) during a period when global climate became much more arid, a change that has lasted until today (13). In fact, the current Mediterranean climate emerged during the Quaternary (8), corresponding with the extinction of a substantial component of Tertiary taxa. Based on paleobotanical evidence (9, 10), the archetypal evergreen sclerophyllous vegetation of modern Mediterranean-type vegetation is relictual of the Madrean-Tethyan vegetation of the Tertiary, which originally existed in a belt around North America and Eurasia where the climate was warm and wet climate. Relictual Madrean-Tethyan taxa, or the Laurisilva, can be observed today in the isolated northern Atlantic Canary archipielago (9, 14). During most of the Tertiary, sclerophyllous shrubs constituted the understory of a rich oak-laurel-madrone woodlands, and these shrubs expanded geographically in response to the drying climate during the Eocene (55 Myr B.P.) and the Oligocene (36 Myr B.P.) (9, 10). Despite the wave of extinctions that occurred with increasing aridity, the fossil record shows that large taxonomic components of this ancient flora remain in contemporary communities of Mediterranean regions (3, 9, 10) and tropical non-Mediterranean regions (13, 15) around the world and include some of the most abundant modern genera

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Abbreviations: Myr, million years; OU, Ornstein–Uhlenbeck.

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such as *Rhus*, *Cercocarpus*, *Garrya*, *Ceanothus*, *Arctostaphylos*, *Pistacia*, *Quercus*, and *Dodonaea.*

As groups, Tertiary and Quaternary taxa differ substantially in life-history and reproductive traits (3, 13). Indeed, analysis of life history-reproductive traits across woody genera in Mediterranean ecosystems indicates two sharply contrasting life-history syndromes that are consistently associated with evolutionary origin (3, 13). The most important traits distinguishing Tertiary and Quaternary syndromes are fruit type (fleshy vs. nonfleshy fruits) and seed size, which are directly related to the regeneration niche (3). Many fleshy-fruited Tertiary species have been reported to depend of the facilitative effects of other species to establish (12, 16). In contrast, dry-fruited Quaternary species often are reported to recruit in open microsites without other species, such as caused by recurrent Mediterranean fires (12). Based on this potential relationship between ancestry and regeneration life history traits, we predicted that: (*i*) facilitation from other plants is crucial for the regeneration of species that evolved during the mesic Tertiary, (*ii*) species that evolved during the arid Quaternary do not depend on facilitation from other species and act as beneficiaries for Tertiary species.

For taxa in Mediterranean climates that could be identified as having either Tertiary or Quaternary lineages, we analyzed studies published from 1940 to the present and that had been conducted in California, Mediterranean Basin, Chile, South Africa, and Australia (Table 1, which is published as supporting information on the PNAS web site). Specifically, we searched the ecological literature for data on the regeneration niches of species (those requiring facilitation from a nurse or not), and the paleobotanical literature for the periods in which particular taxa arose. For a broader comparative analysis and an internal methodological control for our compilation of the ecological literature, we also collected paleobotanical data from the literature on "Mexical" shrubland of the Tehuacán Valley, central Mexico, and then measured for ourselves the regeneration niches of all species for which we could find paleological data. Mexical occurs along the main mountain ranges of Mexico, is semiarid (but with summer precipitation), and shares a tropical, Tertiary history with Mediterranean-climate areas (15). Therefore, incorporating the Mexical into our study also allowed a comparison of recruitment patterns between Tertiary and Quaternary taxa in a region that has experienced strong aridification but without a Mediterranean climate. In summary, research in the Mexical was intended to (*i*) determine whether ecological literature analyses were corroborated by field measurements and (*ii*) determine whether vegetation with the same evolutionary history but a different climatic history showed similar relationships between recruitment life history and periods of taxonomic origin. Detailed environmental information regarding this study site is presented in ref. 15.

In addition to direct analyses of taxonomic origin based on the fossil record, we conducted a second analysis of recruitment niche based on whether modern taxa demonstrate a large-seeded, fleshy-fruited syndrome or a small-seeded dry-fruited syndrome under the corollary that the first syndrome correspond to Tertiary lineages while the second one correspond to Quaternary lineages. Therefore, delineating the taxa by syndrome allowed an ecological examination of the relationship between period of origin and recruitment strategy in those regions. For the Mediterranean areas and the Mexical, we conducted two types of 2 × 2 contingency tables according to the following criteria: (*i*) by using the taxa in which the age was assessed by means of paleobotanical databases and (*ii*) by using the Tertiary and Quaternary syndromes described in refs. 3 and 13.

Results and Discussion

Regeneration Niche of Lineages. Our analyses indicate that facilitation, or the "nurse" effect, is much more important for the recruitment of species that evolved in the Tertiary period than for the recruitment of species that evolved in the Quaternary period. Of the 113 taxa across all six examined regions that were identified as evolving during the Tertiary from the fossil record, 86 were identified in the literature (or measured by us) as recruiting significantly more beneath the canopies of other species than in the open (Table 1 and Fig. 1, for all regions combined $X^2 = 103.3$; $P < 0.0001$). In contrast, taxa that were identified from the fossil record as evolving in the Quaternary recruited preferentially in open spaces and avoided the canopies of other species; 97 of 100 Quaternary species recruited in the open rather than under nurse plants. This pattern was most pronounced in California ($X^2 = 27.06$; $P < 0.0001$), the Mediterranean basin ($X^2 = 40.44$; $P < 0.0001$), Chile ($X^2 = 8.12$; $P = 0.018$), and the Mexical ($X^2 = 18.17$; $P < 0.0001$). South Africa ($X^2 = 4.54$; $P = 0.067$) and Australia (data did not allow to run the X^2 test) showed a less pronounced pattern. In contrast with other Mediterranean areas of the world, information on regeneration requirements of species is more limited for South African and Australian floral elements, and there is an insufficient fossil record to date the radiation of different groups (17, 18).

We found the same pattern when we classified taxa by using the modern syndromes described above (Table 1; see also Fig. 3, which is published as supporting information on the PNAS web site). Taxa demonstrating a Tertiary syndrome recruited far more commonly beneath nurse plants, with 97 of 100 Tertiary-syndrome taxa requiring facilitation (for all regions combined $X^2 = 186.3$; $P < 0.0001$). In contrast, 128 of the 139 taxa demonstrating a Quaternary syndrome recruited in open spaces and did not require facilitation from other species. This pattern was strongly significant in all examined regions of the world: California ($X^2 = 29.72$; $P < 0.0001$), the Mediterranean basin ($X^2 = 40.35$; $P < 0.0001$), Chile ($X^2 = 10.88$; $P = 0.002$), South Africa ($X^2 = 18.24$; $P < 0.001$), Australia ($X^2 = 42.00$; $P < 0.001$), and the Mexical ($X^2 = 37.3$; $P < 0.0001$). Importantly, field-based measurements of recruitment strategy in the Mexical corroborated literature-based analyses.

In sum, modern regeneration niches (19) and recruitment life history strategies of taxa derived from the ancient Madrean-Tethyan flora and the recent Quaternary are highly correlated with the time and environment in which these taxa evolved. The connection between evolutionary history and ecological function also is emphasized in successional studies that indicate a clear correlation between the age in which taxa originated and the stage of colonization in which the taxa participate. Quaternary species are by far the most common early colonizers of open areas in Mediterranean climate vegetation, comprising 35 of 43 early successional species identified in the literature (Table 2, which is published as supporting information on the PNAS web site). In contrast, of 49 late successional species identified in the literature, 48 were Tertiary elements. In other words, Tertiary taxa become important components of communities in semiarid climates only after more drought-tolerant Quaternary species have created mesic conditions. Although Tertiary species also can recruit under Tertiary plants, the most common nurses consist of Quaternary species, especially early in the succession. This idea is supported by the large facilitation experiment performed by Gómez-Aparicio *et al.* (20), who demonstrated that pioneer (i.e., Quaternary) shrubs facilitate the establishment of woody, late-successional (i.e., Tertiary) Mediterranean species. Tertiary taxa seldom recruit by seed in the first several decades after fire, and, therefore, these taxa require long fire-free periods for establishment, which almost exclusively occur after closed-canopy stands have developed (12). Fire is less important in Chilean matorral than in Californian chaparral (21). However, in the matorral, Quaternary species are overwhelmingly the first colonizers of postagricultural and abandoned pasture land, and are followed by Tertiary elements. The same pattern has been reported for different regions of Europe

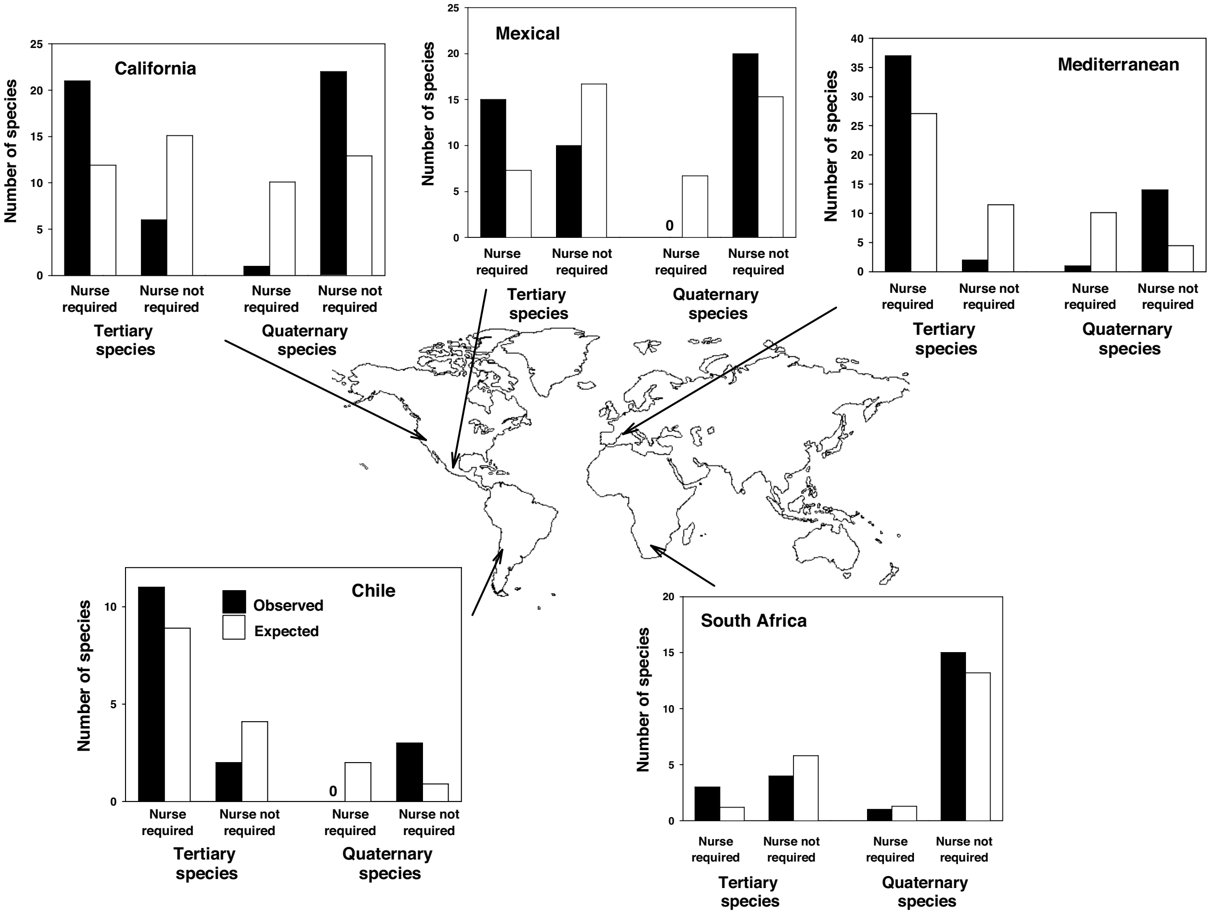

Fig. 1. Regeneration-niche requirements of Tertiary and Quaternary lineages, based on the fossil record, in the five Mediterranean areas of the world and in the Mexical shrubland of central Mexico. Filled bars show the observed numbers of species from each lineage reported in the literature that occupy particular regeneration niches, and open bars show the expected numbers of species of each lineage.

after cessation of coppicing and grazing in recent decades (22, 23). Likewise, studies of large-scale vegetation dynamics demonstrate that Tertiary species colonize vegetation dominated by Quaternary species in Mediterranean climates throughout the world (Table 3, which is published as supporting information on the PNAS web site). From this successional evidence, it is clear that the key role of Quaternary species for the maintenance of Tertiary species was crucial during the climatic fluctuations in the Southern and Northern hemispheres occurred during the Quaternary (24, 25), which resulted in altitudinal or geographical vegetation shifts.

Regeneration Niche Conservatism. Despite the effects of climate change, evolution, and culling processes on contemporary communities, fossils show that the ecological traits of many extant species in Mediterranean ecosystems have remained similar for millions of years (2, 13, 15, 26). In other words, many ecological characteristics of ancient taxa appear to be highly conserved over geological time scales. This fact raises the possibility that facilitative effects of ancient Tertiary lineages by modern Quaternary lineages not only conserve species, but also conserve specific ancient traits (2). Therefore, to test whether ancient traits of Tertiary taxa have been maintained by stabilizing selection through the facilitation, we mapped an index of the regeneration niche (the percentage of seedlings recruited under shrubs) for each Mexical species in a phylogenetic tree and compared the fit of several models of evolution, each depicting a different selective regime as explained below (Fig. 2). Character associations mapped in a phylogenetic tree assembling the species that comprise a particular community, such as we have performed here, reflects not only the evolutionary history of the traits but also the sorting and assembly processes acting in such a local community (27). Thus, this method is an excellent procedure to explore how the regeneration niche of extant lineages may have been sorted by changes in climatic conditions over time.

For our data, a simple evolutionary model accounting for stabilizing selection [Ornstein–Uhlenbeck (OU) with a single optimum] explained the observed regeneration niche (i.e., the percentage of plants recruited under shrubs) of Mexical plant species much better than the neutral Brownian motion model (LRtest = 10.66; df = 2; P = 0.004). The fit of the stabilizing selection model was significantly improved (LRtest = 11.09; df = 2; P = 0.004) when two different optima were allowed for the regeneration niche: one for Tertiary and another for Quaternary lineages. Whereas Tertiary lineages reached the optimum at 90% of plants recruiting under shrubs, Quaternary lineages achieved this optimum at 13%.

The highly consistent fleshy-fruited life history trait among Tertiary species probably plays a crucial role in the ancient lineage-modern recruitment relationship. Fleshy fruits drive dispersal from the parent to understory environments because birds deposit highly disproportionate numbers of seeds where they perch (28). However, dispersal to shrubs alone cannot explain the patterns we describe here, and many studies (including those of species considered here) have shown that the canopies of species from the Quaternary have direct positive

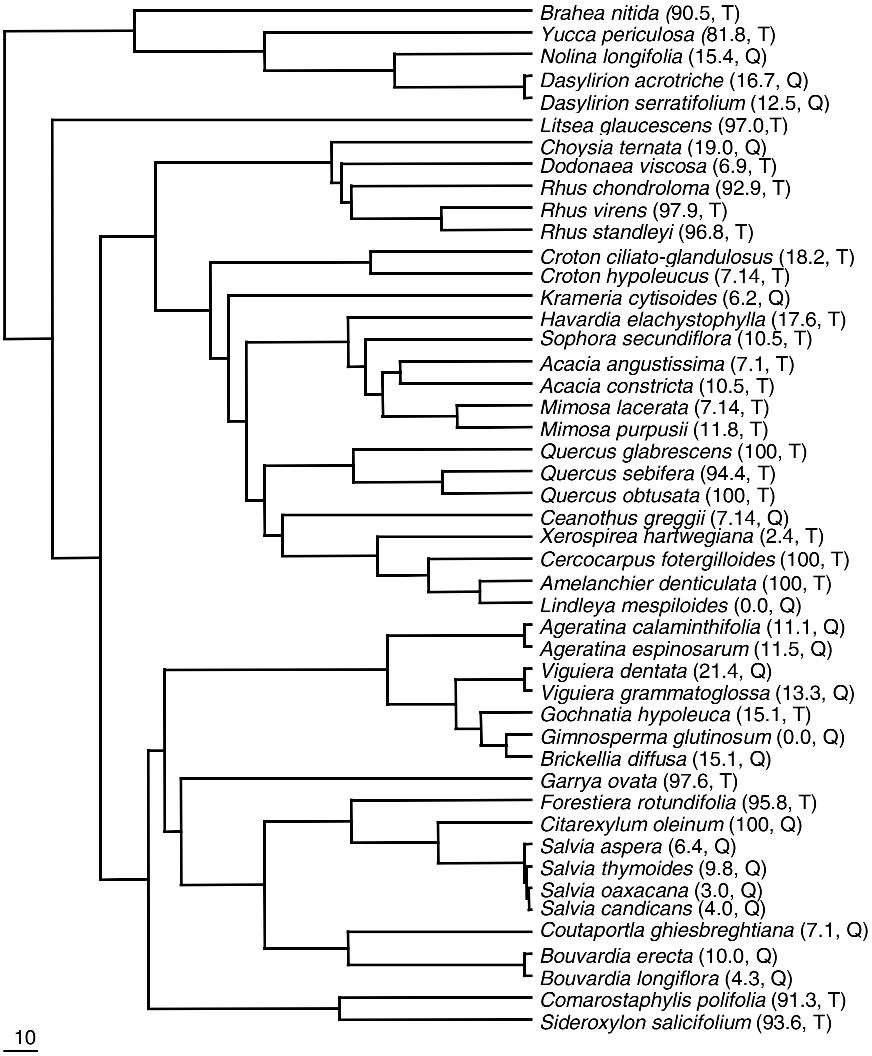

Fig. 2. Phylogenetic tree for species in the Mexical shrubland. The scale for the branches is presented in millions of years (Myr). Values associated with each species show the percent of young individuals recruiting beneath the canopy of perennial nurse plants. T, Tertiary lineage; Q, Quaternary lineage.

effects on Tertiary species below them through shade, maintenance of soil moisture, and local fertilization effects (12). The importance of these direct effects indicates that the ancient lineage-modern recruitment relationships are the product of a long-term conservation of the ecological regeneration niche. Likewise, the high degree of evolutionary conservatism found in many old lineages in Mediterranean vegetation (2) suggests that facilitation has promoted stabilizing selection through evolutionary time. Facilitation provided by Quaternary species during eras when Mediterranean ecosystems experienced climatic fluctuations and altitudinal shifts (8) is a plausible explanation for evolutionary stasis in these systems. By this process, we mean that ancient-lineage species found climatic conditions similar to their ancestral conditions in the more humid, mesic, and shaded conditions under modern drought-tolerant species, thus avoiding either extinction or strong selection to adapt to modern climate.

Ecophysiological Correlates. Lineage–life history relationships correspond with several general morphological and ecophysiological differences among Tertiary and Quaternary taxa (Table 4, which is published as supporting information on the PNAS web site). First, Tertiary taxa have much larger leaves with greater mass per leaf area than Quaternary taxa. Tertiary taxa are almost exclusively evergreen (several oak species are not), whereas most Quaternary species are drought deciduous. In a comparison of Tertiary species and Quaternary species found in the literature, the maximum root length of Tertiary species in field measurements was 9.0 ± 2.9 m ($n = 9$) compared with 2.7 ± 0.4 m ($n = 11$) for Quaternary species ($t = 2.34$, $P = 0.031$; Table 4). Facilitation may be crucial for seedlings of species that cannot survive in full sunlight before their roots reach a consistent water supply. Tertiary species are also more likely to develop large storage structures called burls or lignotubers. Based on a literature search, most Quaternary species also tolerate much lower water potentials (-5.7 ± 0.7 MPa, $n = 18$) than Tertiary species (-3.1 ± 0.3 MPa; $n = 37$; $t = 4.89$, $P < 0.001$). These physiological and anatomical differences between Quaternary and Tertiary taxa match the open, harsh recruitment niches of the former and the comparatively mesic and cool subcanopy recruitment niches of the latter.

Community Ecology Implications. The relationship between recruitment life history and evolutionary lineage has important and previously undescribed implications for our understanding of the development and sustenance of global biodiversity in arid regions. First, these results suggest that ancient components of modern Mediterranean-climate flora may not exist today without the long-term positive effects of recently evolved species and that facilitative ecological relationships play an important role in the preservation of global biodiversity over evolutionary time scales: Modern plant taxa sustain ancient plant taxa. Second, our results suggest that the processes that develop regional floras, even at continental scales, may not be fully described by neutral models (5).

Our results suggest that facilitation has played a crucial role in maintaining biological diversity through evolutionary time. Community-scale facilitation appears to have been a crucial historical sorting process sustaining ancient species in semiarid plant communities as the globe has become more arid. As the Earth became drier, facilitation by Quaternary species appeared to have provided microsites that closely matched the ancestral conditions of ancient drought-intolerant lineages. By doing this nursing, Quaternary species may have stabilized selection and contributed to the maintenance of ancestral traits of Tertiary lineages. As argued by Ackerly (2), competing (Tertiary) species occupied habitats and microsites that closely matched conditions to which they were previously adapted, conditions that our evidence indicates were provided by modern taxa.

Our results have important implications for the response of species and communities to climate change. Davis *et al.* (29) warned that most attempts to predict biotic responses to climate change inappropriately assume that the species' responses can be understood in the context of a ‘‘climate envelope,’’ in which the distribution of a species is determined by its adaptation to particular climatic conditions. But it is clear from our results that the effects of climate change on the distributions of species also will be determined by interactions with other species (30). Our results indicate that facilitative interactions among plants over millions of years have been a central determinant of current community composition and diversity and are likely to do so as climate changes in the future.

Methods

Lineage-Age Assessment. For all six regions, the Quaternary or Tertiary lineage of each taxa was obtained from a database (3, 9, 10, 13) (and from references in ref. 13) by determining whether genera were present or absent in the pre-Pliocene fossil record and/or the presence or absence of biogeographical disjunctions (Table 1).

The relevant age for our analyses is that of the crown and not the stem group. For example, both *Ceanothus* subgenera originated >18 Myr ago (i.e., the stem group is Tertiary) but radiated recently (i.e., the crown group is Quaternary) (31). Because we are interested in the current traits of the species evolving in the Tertiary vs. Quaternary, the proper age assignment must be done to the crown group. Similarly, a fossil-calibrated phylogeny of *Salvia* helped us to identify which crown groups evolved during the Tertiary or Quaternary (32). In the absence of fossil-calibrated phylogenies to identify recent splits of crown groups, we stuck to the criteria explained above based on fossils and biogeographical disjunctions.

Although we could not detect whether the current traits evolved before (i.e., preadaptation) or after (i.e., adaptation) the radiation of the crown group along the Tertiary-Quaternary transition (31), this is not a problem for the ecological interpretation of our analysis because the relevant feature is that taxa diversifying along the Quaternary have different traits to taxa diversifying in the Tertiary, irrespective of the preadaptive or adaptive nature of such traits.

Recruitments Patterns in the Mexical Shrubland. In the Mexical, we measured the total cover of perennial plants and the cover of open space in a 4,800 m^2 area. For each species we counted the number of young individuals growing beneath canopies and in open spaces. We then constructed a two by two contingency analysis for each species with the observed number of young individuals growing beneath plant canopies versus in open areas compared with the expected number of individuals derived from the proportions of area occupied by vegetation versus open space.

Correlating Evolutionary History with Regeneration Niche. ***The phylogenetic tree.*** The phylogenetic tree assembling Mexical species was developed with the help of the program Phylomatic as implemented in Phylocom 3.34b (www.phylodiversity.net/phylocom). This program returns a working phylogenetic tree after matching the genus and family names of our study species to those contained in the angiosperm megatree (R20050610.new). This megatree is based on the work of the Angiosperm Phylogeny Group and represents a constantly changing picture of the evolution of plants.

The few polytomies that created our working tree were resolved on the basis of other published phylogenies (33) for the relationship among Rutaceaee, Anacardiaceae, and Sapindaceae: Relationships within Rosaceae are at the Dickinson Laboratory home page at www.botany.utoronto.ca/faculty/dickinson/DickinsonLab.html, the relationship among Fabales, Fagales, and Rosales is in ref. 33), and the relationship among Malphigiales, Eurosids I, and Rosids is in ref. 34. When no information was available to resolve the polytomies, we resolved them randomly, as for *Rhus* (three species), *Quercus* (three species), *Salvia* (four species), and Asteraceae (five species). The values of the regeneration niche of closely related species resulting from such random resolutions were very similar; therefore, the result of the final comparative test of regeneration niche was highly robust to the topological uncertainty. We verified topological robustness by rerunning all of the analyses in five trees in which polytomies were resolved differently (results not shown).

The branch lengths of our phylogenetic tree were adjusted with the Bladj algorithm in the Phylocom 3.34b program (www.phylodiversity.net/phylocom). This method takes the age estimates for major nodes in our tree from Wikstrom *et al.* (35), and distributes undated nodes evenly between nodes of known ages. We included the following age estimates on the basis of the fossil records found in the literature: *Acacia* (40 Myr), *Amelanchier* (55 Myr), *Cercocarpus* (40 Myr), *Comarostaphylis* (55 Myr), *Dodonaea* (40 Myr), *Forestiera* (24 Myr), *Garrya* (24 Myr), *Rhus* (55 Myr), *Sideroxylon* (30 Myr), and *Sophora* (24 Myr). We also assigned all Quaternary species the age of 2 Myr. Although this method must be treated as a rough approximation, it produces a pseudochronogram that allows estimating phylogenetic distance (in units of time) between taxa for the analysis of community phylogenetic structure.

The model of evolution. Most of the comparative methods assume a neutral model of evolution, called ‘‘Brownian motion,’’ which is not suitable for the study of phenotypes evolving under stabilizing selection, but only phenotypes evolving under the influence of pure drift and natural selection in rapidly and randomly changing environments (36). The model of adaptive evolution that accounts for stabilizing selection is the OU process (35), also described as a ‘‘rubber-band’’ process, in which the mean phenotype is held near a fixed optimum but random drift simultaneously causes fluctuation around the optimum. Selection acts like a rubber band, tending to return the population to the peak, such that the pull toward the optimum is stronger as the phenotype drifts further away. The main parameter of the OU model is the magnitude of the restraining force (α) that can be interpreted as a measurement of stabilizing selection and also as a rate of adaptation (35). The model also allows the calculation of one or multiple selective optima for a trait, θ.

Three models reflecting the following selective regimes were tested as proposed by Butler and King (37).

Model 1: Brownian motion (BM): The regeneration niche evolves after a pure drift process and natural selection in rapidly and randomly changing environments.

Model 2: OU with a global optimum (OU1): The regeneration niche evolves under stabilizing selection toward a single global optimum for all of the lineages.

Model 3: OU with two global optima (OU2): The regeneration niche evolves under stabilizing selection toward two different optima, one for Tertiary and another one for Quaternary species.

The logit transformation was applied to the dependent variable (percentage of seedlings recruited under shrubs) and each species was labeled as Tertiary or Quaternary as previously explained. The Brownian motion model was nested within the OU1 model because both models are identical when $\alpha = 0$. Similarly, the OU1 model was nested within OU2 because both models are identical when the trait optima do not differ. Thus, we could compare the fit of the nested models by means of the likelihood ratio test assuming a χ^2 distribution.

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