

PHYLOGENY AND THE HIERARCHICAL ORGANIZATION OF PLANT DIVERSITY

JONATHAN SILVERTOWN,^{1,4} MIKE DODD,¹ DAVID GOWING,¹ CLARE LAWSON,² AND KEVIN MCCONWAY³

¹Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA UK

²Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, The University of Reading, Earley Gate, P.O. Box 237, Reading, RG6 6AR UK

³Department of Statistics, The Open University, Walton Hall, Milton Keynes, MK7 6AA UK

Abstract. R. H. Whittaker's idea that plant diversity can be divided into a hierarchy of spatial components from α at the within-habitat scale through β for the turnover of species between habitats to γ along regional gradients implies the underlying existence of α , β , and γ niches. We explore the hypothesis that the evolution of α , β , and γ niches is also hierarchical, with traits that define the α niche being labile, while those defining β and γ niches are conservative. At the α level we find support for the hypothesis in the lack of close significant phylogenetic relationship between meadow species that have similar α niches. In a second test, α niche overlap based on a variety of traits is compared between congeners and noncongeners in several communities; here, too, there is no evidence of a correlation between α niche and phylogeny. To test whether β and γ niches evolve conservatively, we reconstructed the evolution of relevant traits on evolutionary trees for 14 different clades. Tests against null models revealed a number of instances, including some in island radiations, in which habitat (β niche) and elevational maximum (an aspect of the γ niche) showed evolutionary conservatism.

Key words: coexistence; community assembly; diversity; evolutionary lability; geographical range; habitat; hydrology; niche overlap; plant community; plant phylogeny.

INTRODUCTION

R. H. Whittaker (1975) proposed that diversity should be analyzed at a hierarchy of spatial scales. At the local scale, α diversity represents the number of species found within a habitat. These species occur in sufficient proximity to interact with one another. At intermediate scales, β diversity quantifies the turnover in species that takes place between habitats or along environmental gradients. At a still wider scale, γ diversity is the species diversity of a region. Of α and β diversity, Whittaker (1975:119) wrote that they "will be recognized as consequences of niche differentiation and habitat diversification of species, respectively." Not long afterwards, Pickett and Bazzaz (1978) explicitly referred to these concepts as the α niche and the β niche. (A glossary of terms is given in Table 1.) Although these terms were not widely adopted when they were first introduced, recent research on the phylogenetic structure of ecological communities suggests that the distinction between α and β niches should receive greater attention, because the hierarchical relationship between them might reflect the hierarchical structure of evolutionary trees (Fig. 1).

For a given phylogeny, heritable traits that vary freely among the terminals (tips) of the tree are likely to be

evolutionarily labile. If these traits determine a species' niche, community structure will appear free of phylogenetic conservatism. In contrast, traits that vary little among terminals on the same tree indicate that their evolution is likely to be more conservative. Niche-related traits of this kind can potentially produce a phylogenetic signal in the structure of ecological communities. Whether conservatively evolving niche traits actually do produce this signal depends upon the ecological processes of community assembly that determine how many representatives of a conservatively evolving clade are present. In areas of high endemism such the Cape Floristic Region of South Africa or oceanic archipelagos such as Hawaii, some communities might have been assembled, at least in part, by adaptive radiation in situ. This is where we might expect to find recent evolutionary events influencing community structure most strongly. However, this form of community assembly is a rare event, and most plant communities, including some on islands such as those in Macaronesia (Santos 2001), have been assembled from plants with quite disparate phylogenetic histories (Pennington et al. 2004, Pennington and Dick 2004).

We ask two central questions. First, do ecological traits evolve in a conservative manner? Second, is there a difference in evolutionary lability between the traits that underlie α and β niches? Recent studies of the phylogenetic distribution of ecological traits have tended to emphasize the conservative nature of plant trait evolution and suggested that this influences community assembly (Tofts and Silvertown 2000, Webb 2000,

Manuscript received 18 January 2005; revised 9 September 2005; accepted 13 September 2005. Corresponding Editor (ad hoc): C. O. Webb. For reprints of this Special Issue, see footnote 1, p. S1.

⁴ E-mail: J.Silvertown@open.ac.uk

TABLE 1. Definitions of terms used in the text.

Term	Definition	Source
α niche	The region of a species' realized niche corresponding to species diversity at the local (α) scale where interactions among species occur	2, 5
β niche	The region of a species' niche that corresponds to the habitat(s) where it is found; equivalent to the "habitat niche" Grubb (1977)	2, 3
γ niche	The geographical range of a species	6
Community	The collection of species that predictably co-occurs within a particular type of habitat	
Habitat	The kind of environment where a species occurs, defined largely by physical conditions; note that conditions will usually be influenced by organisms as well as physical factors, but direct interactions among organisms are not used to define habitats	2
Lability	The property of evolutionary changeability in a trait	
Niche	An n -dimensional hypervolume defined by axes of resource use and/or environmental conditions and within which populations of a species are able to maintain a long-term average net reproductive rate ≥ 1	1, 4
Niche trait	A measurable property of a species, by which its niche (α , β , or γ) can be defined	
Realized niche	The region of its niche that a species is able to occupy in the presence of interspecific competition and natural enemies	1

Sources: 1, Hutchinson (1957); 2, Whittaker (1975); 3, Pickett and Bazzaz (1978); 4, Chase and Leibold (2003); 5, Silvertown (2004); 6, Silvertown et al. (2006).

Prinzing et al. 2001, Webb et al. 2002, Ackerly 2003, 2004, Chazdon et al. 2003). One example of this pattern is the long-standing observation that, in many communities, there is a higher ratio of species per genus than would be expected if communities were assembled by random draws from the species pool (e.g., Williams 1964). If congeneric species are overrepresented in communities, then it follows that they must share ecological traits that influence community assembly and that these traits evolve more slowly than the rate of appearance of new species.

Other studies, however, suggest that some traits that influence community structure do not evolve conservatively. Cavender-Bares et al. (2004) detected labile evolution in the soil moisture tolerances of North American oak species and found that these species segregated along soil moisture gradients. Silvertown et al. (1999) found that plant species in English meadow grasslands also segregated on hydrological gradients and later reported that there is no correlation between the ecological distance between species in hydrological niche space and their phylogenetic distance as measured by the evolution of the *rbcL* gene (Silvertown et al. 2006). How can these data be reconciled with the many other examples of the conservative evolution of ecological traits?

Silvertown et al. (2006) suggested that the apparent contradiction between the lack of phylogenetic signal in their data, which implies evolutionary lability in hydrological niches, and contrary findings by other authors implying conservative evolution in some traits could be explained if the traits have different evolutionary lability. They proposed that habitat-determining traits that influence β diversity, and which may be said to define the β niche (Pickett and Bazzaz 1978), evolve conservatively. By contrast, traits involved in coexistence and that influence α diversity, defining the α niche, are evolutionarily labile. Such a pattern could arise if, as most theories of coexistence demand (Chesson 2000), species must differ from each other in order to coexist. The

corollary of this is that α niches and coexistence will necessarily be determined by labile traits. In short, Silvertown et al. (2006) proposed that competing species must share β niches in order to occur in the same habitat, but they must have different α niches in order to coexist.

Silvertown et al. (2006) proposed that, by extension of the relationship between α and β niches and Whittaker's (1975) α and β diversity, the geographical range of a species can be regarded as its γ niche. Thus, there is a hierarchy of three niche levels with γ at the top (Fig. 1). The little evidence that is so far available suggests that β niche traits are evolutionarily conservative; data pertaining to the evolution of the γ niche are even more sparse.

Prinzing et al. (2001) analyzed the niches of European plant species using Ellenberg indicator values (Ellenberg 1979, Ellenberg et al. 1991) and found strong evidence of evolutionary conservatism. These values were devised to quantify on an ordinal scale where different plant species are found in central Europe along major environmental axes, such as soil moisture, pH, light, and soil fertility. Several studies have found that Ellenberg values are stable traits that consistently predict the β niche of species across Europe more generally (Thompson et al. 1993, Hill et al. 2000, Schaffers and Sykora 2000, Prinzing et al. 2002). Ellenberg values can be regarded as β niche traits, because they refer to large-scale environmental gradients. However, since α niches are nested within β niches, some correlation between traits like soil moisture tolerance is to be expected.

Ackerly (2004) examined phylogenetic conservatism in the evolution of leaf traits that are associated with adaptation to Mediterranean climates in California chaparral habitat. These are a good example of traits associated with the β niche. Specific leaf area was significantly conserved in all four families analyzed, and leaf size in three. These results suggest that sclerophylly and other leaf traits associated with Mediterranean habitats evolved before California chaparral was colo-

nized, supporting the view that the β niche traits evolve in a conservative manner.

Very little evidence is available concerning the evolution of γ niches. Qian and Ricklefs (2004) found that the latitudinal ranges, and hence γ niches, of 57 plant genera with disjunct distributions in North America and Asia were correlated between continents, suggesting that the genera had highly conserved γ niches that dated to before the origin of the disjunctions, perhaps 18 million years ago in the case of woody species. How typical this result will prove to be of γ niches in general is not clear at present.

Other studies have examined the degree of range overlap between members of the same clade (Barraclough and Vogler 2000, Graham et al. 2004). Barraclough and Vogler (2000) found that in a range of vertebrate and insect phylogenies range overlap was low between recently diverged taxa, but increased with time since divergence. This indicates that speciation occurs more often in allopatry (no range overlap) than sympatry, but does not directly address the issue of γ niche evolution, since ranges can be split (i.e., become allopatric) by the appearance of environmental barriers, without any need for evolutionary change in the γ niche.

In this paper we present four new lines of evidence that have a bearing on the evolutionary conservatism of α , β , and γ niche traits. Each piece of evidence applies a different kind of test, as appropriate to the data available.

First, we take a closer look at the English wet meadow communities in which Silvertown et al. (2006) found α niche traits to be evolutionarily labile. We perform a new analysis of the data in which we ask whether groups of specialists that are confined to particular subcommunity types are more closely related to one another than would be expected for randomly drawn samples from the same community. A smaller phylogenetic distance between specialists than between randomly drawn nonspecialists would imply evolutionary conservatism in the specialist group.

Second, we reanalyze published data on various ecological traits in a number of plant communities to determine whether α niche overlap between congeners is greater or less than between noncongeners in the same community. Although we recognize that there is no consistent phylogenetic definition of a genus, and that some may be very old, congeners can usually be expected to be more closely related than species from other genera drawn from the same community. Trait variation ought therefore to be smaller between congeners than noncongeners for conservatively evolving traits that predate the origin of the genus, but similar for labile traits.

Third, we conduct a test of a prediction derived from the hypothesis that β niche evolution is conservative by examining the number of inferred transitions in habitat (reflecting the β niche) within plant phylogenies for a sample of 12 independent clades. Changes of habitat should be fewer than expected by chance if β niche

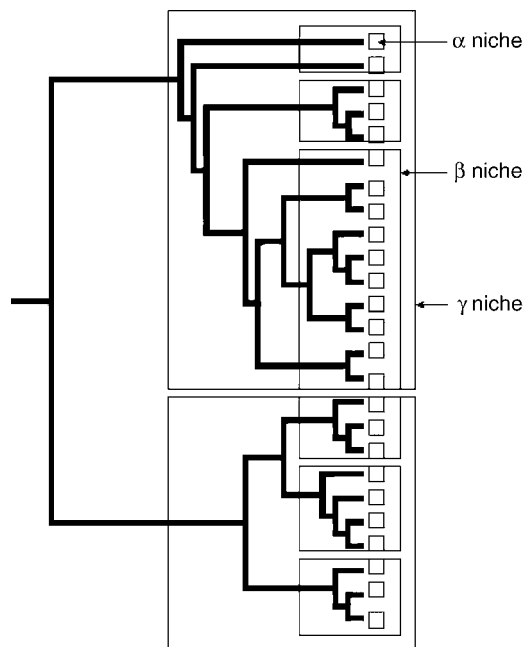


FIG. 1. A Venn diagram showing the nested hierarchy of α , β , and γ niches superimposed upon a hypothetical phylogenetic tree. Note that the rectangles representing each kind of niche intersect the phylogenetic tree at progressively deeper levels from α to β to γ niches, indicating earlier origin and greater conservatism.

evolution is conservative. As a subsidiary hypothesis, the expected patterns of conservatism should be stronger in clades that have evolved in continental areas, where available habitats are likely to have been already occupied by competitors, than in clades that have radiated on islands where most habitats were unoccupied.

Finally, we apply the same kind of test to γ niche evolution by optimizing maximum elevation (reflecting the γ niche) onto phylogenies for two clades.

METHODS

Are habitat specialists phylogenetically clustered?

Silvertown et al. (1999, 2001) previously analyzed the niche relationships of species in two mesotrophic grassland (meadow) plant communities classified as MG5 and MG8 by the British National Vegetation Classification (Rodwell 1992). Silvertown et al. (2001) suggested that some of the niche separation observed in these communities arose as deep as the split between monocots and eudicots, indicating that niche specialization occurs within particular clades. For the present study, we identified specialists from within each of the two community types using data from an extensive survey made by Gowing et al. (2002). This survey recorded an estimate of percent cover of all species present in 3904 1×1 m quadrats across 18 sites representative of MG5, MG8, and other floodplain hay meadow types in England. Quadrats were classified into 12 communities

TABLE 2. Comparison of α niche overlaps between congeneric pairs of herb species in nine genera and mean overlaps between the congeners and species in other genera.

Genus	Total no. overlapping species	Overlap with congeners	Comparison	Overlap with noncongeners	α niche axes	Data source
<i>Drosera</i>	9	0.00	<	0.60	water table gradient in a bog community	5
<i>Prosopis</i>	16	0.15	<	0.38	soil moisture and nutrients in a desert community	4
<i>Dentaria</i>	17	0.42	>	0.37	forest understory microtopography and light	1
<i>Galium</i>	17	0.45	=	0.45	forest understory microtopography and light	1
<i>Senna</i>	16	0.48	>	0.31	soil moisture and nutrients in a desert community	4
<i>Trillium</i>	17	0.51	<	0.52	forest understory microtopography and light	1
<i>Aster</i>	10	0.76	>	0.44	phenology and microtopography in forest understory	2
<i>Helictotrichon</i>	10	0.87	>	0.83	shoot phenology in grassland	3
<i>Festuca</i>	10	0.88	>	0.83	shoot phenology in grassland	3

Notes: There is no significant difference overall between the degree of overlap found between congeners and the overlap between noncongeners (Wilcoxon matched-pairs test, $Z = 0.42$, $P = 0.67$).

Sources: 1, Mann and Shugart (1983); 2, Beatty (1984); 3, Sydes (1984); 4, Shaukat (1994); 5, Nordbakken (1996).

and subcommunities using the program TWINSpan (Hill 1979).

A group of seven species characteristic of the MG5a subtype of the MG5 community consisted of *Trifolium pratense* (Fabaceae), *Rhinanthus minor* (Scrophulariaceae), *Dactylis glomerata* (Poaceae), *Prunella vulgaris* (Lamiaceae), *Heracleum sphodylium* (Apiaceae), and *Leucanthemum vulgare* and *Leontodon saxatilis* (both Asteraceae). Within the MG8 community type, 10 species were identified as specialists associated with a *Carex disticha* subcommunity. These were *Carex disticha*, *C. distans*, and *Eleocharis uniglumis* (Cyperaceae); *Senecio aquaticus* and *Bellis perennis* (Asteraceae); *Juncus inflexus*, *J. articulatus*, and *J. subnodulosus* (Juncaceae); *Festuca arundinacea* (Poaceae), and *Trifolium fragiferum* (Fabaceae). Specialists occurred more frequently in the designated subcommunity types (MG5a, MG8 *C. disticha*) than in any other of the 12 communities identified in the TWINSpan analysis.

Phylogenetic distances between all pairwise combinations of 52 species belonging to MG5 and MG8 communities were calculated by Silvertown et al. (2006). Distances were calculated as the sum of branch lengths connecting species in a tree fitted to *rbcL* sequences using maximum likelihood in PAUP* (Swofford 1996). For each of the two specialist groups, we computed the mean and variance of pairwise phylogenetic distances among members of the group and compared these with expected (null) distributions produced by randomization. Null distributions were derived by sampling groups of n species at random from the 52 species in the meadow species pool for which *rbcL* sequences are known, where n was the number of species in the specialist group. To avoid bias in the species pool caused by underrepresentation of sequences for *Carex* and *Juncus*, we added extra copies of *rbcL* sequences for species in these genera when conducting the test on the *Carex disticha* subcommunity type. Using substitutes in this way does not introduce bias, because *rbcL* sequence differences among species of *Carex* and among *Juncus* species are very small. A total of 10^4 randomizations were

run for each null model. If specialists are significantly clustered phylogenetically, then the mean and variance of pairwise *rbcL* distances should fall in the lower 5% of values in the null distribution of each statistic.

α niche overlap among congeners vs. other species

Through an extensive review of the literature on plant niches, we identified five studies of plant communities from which it was possible to compute α niche overlaps within and between genera. There were nine sets of congeners in total. The validity of generic names was checked against the online versions of Clayton and Williamson (2003) for grasses and Brummitt (1992) for other species. A name change affected one genus (*Dentaria* to *Cardamine*), but did not alter the implied evolutionary relationships between this genus and the rest of the community with which it was compared. Niche axes varied between studies (Table 2), but overlap was measured using Pianka's index in all cases (Pianka 1973). The pairwise overlap, O_{jk} , between the niche of species j and the niche of species k is

$$O_{jk} = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 p_{ik}^2}} \quad (1)$$

for all resource states, i . In Eq. 1, p_{ij} is the proportion of total resources used by j that consist of resource state i , and p_{ik} is the proportion of total resources used by k that consist of resource state i . Values of O_{jk} range from 0 to 1. The difference in mean overlap between congeners, and between congeners and the rest of the community, was tested by a Wilcoxon matched-pairs test (Sokal and Rohlf 1995).

β and γ niche transitions

We conducted a search of articles and citations in American Journal of Botany, Systematic Botany, and TreeBASE (University of Buffalo, New York, USA; available online)⁵ to identify molecular phylogenetic

⁵ (www.treebase.org)

studies of plants in which $\geq 50\%$ of the extant species in a clade had been sampled (Tables 3 and 4). Phylogenies with < 20 species were excluded because randomization tests of the kind we used to detect phylogenetic conservatism have low statistical power with sample sizes below this limit (Blomberg et al. 2003). Habitat and elevational data were obtained from the same source as the phylogeny wherever they were given, or from standard floras where they were not (Tables 3 and 4). Habitat is by definition a β niche trait. We treated elevational maximum as a γ niche trait, because it delimits the vertical dimension of a species' range and is clearly related to climate.

Evolution of habitat and elevational maximum (EM) were optimized onto trees using MacClade 3.06 (Maddison and Maddison 1992). Habitat was treated as a polymorphic character for species that were present in more than one habitat type. Elevational maximum was scored as a categorical variable with four classes: 0, $EM \leq 1000$ m; 1, $1000 \text{ m} < EM \leq 2000$ m; 2, $2000 \text{ m} < EM \leq 3000$ m; 3, $EM > 3000$ m. Tests for phylogenetic conservatism were performed by comparing the number of transitions (steps) between habitat or EM states required to account for the observed distribution of habitats among terminal taxa with a null distribution. We obtained a null distribution for the number of habitat or EM transitions to be expected in any given tree by randomly shuffling the observed states among its terminals (Maddison and Slatkin 1991). Using MacClade 3.06, we performed 10^3 randomizations for each tree. The probability that an observed number of steps occurred by chance was the frequency of transitions of the same or smaller value found in the null distribution. Frequencies < 0.05 were treated as evidence of significant conservatism in the evolution of habitat preference or EM. The randomization test we used is normally employed on binary characters, but some of our tests involved more than two niche categories (e.g., four EM classes of the γ niche). In order to test the robustness of our results against the unconventional use of multistate characters, where variables could be combined on the basis of some ecological variable (e.g., dry vs. mesic), we ran tests on data recoded as a single binary character.

RESULTS

Are habitat specialists phylogenetically clustered?

The mean and variance of pairwise *rbcL* distances among the seven specialists in the MG5a community were 0.112 ($P = 0.144$) and 0.0017 ($P = 0.226$), respectively. For the 10 specialists in the *Carex disticha* community, the mean and variance were respectively 0.125 ($P = 0.428$) and 0.0023 ($P = 0.362$). In neither community was the mean or the variance significantly lower than expected by chance; thus the null hypothesis of no phylogenetic clustering among specialists cannot be rejected.

α niche overlap among congeners vs. other species

Table 2 compares α niche overlaps between congeneric pairs of species in nine genera with mean overlaps between the congeners and species in other genera. There is no significant difference overall between the degree of overlap found between congeners and the overlap between noncongeners (Wilcoxon matched-pairs test, $Z = 0.42$, $P = 0.67$).

β and γ niche transitions

Table 3 presents β niche transitions in seven island and five continental clades. There was significant conservatism in the evolution of the β niche in five of the seven island clades and in three of the six continental cases. Habitat factors associated with conservatism included the six major altitudinal zones in the Canary Islands (the principal archipelago of Macaronesia) in the case of the *Aeonium* clade, but not in the *Echium* or *Argyranthemum* clades. When a binary coding of β niche into dry vs. mesic was used, *Argyranthemum* and *Sonchus* did show conservatism, but *Aeonium* and *Sideritis* did not (Table 3). Similar patterns were found in Hawaii, with species in the *Schiedea* clade showing conservative evolution in respect of eight habitat types; this clade and the silversword alliance showed fewer transitions than expected between wet and dry environments (Table 3).

In continental clades, conservatism occurred in both habitat variables (serpentine soils and forest vs. open habitats) analyzed in *Calochortus*, in one of three variables (occurrence in vernal pools) in *Mimulus*, and in preference among four habitat types in *Narcissus* (Table 3). Neither *Linanthus* nor *Primula* clades showed evidence of β niche conservatism.

Of the two clades analyzed for γ niche conservatism, EM evolved conservatively in *Pinus*, but not in *Mimulus* (Table 4). Whether the data were coded as four EM classes or two did not affect either outcome.

DISCUSSION

Collectively, the analyses performed here demonstrate a lack of phylogenetic signal in the ecological structure of communities, but, in contrast, indicate its presence in at least some instances of how speciation populates different habitats and how elevational range evolves. The results support the suggestion that α niche traits are evolutionarily labile, while β and γ niche traits *might* evolve in a more conservative manner. However, there are caveats.

The species in the samples used to examine ecological structure in communities on the one hand and adaptive radiation among habitats and elevations on the other were differently constituted. In the first instance, we measured phylogenetic distances between a collection of species that had passed through the various ecological filters involved in community assembly. This resulted in an extremely rarefied sampling of disparate branches of the angiosperm phylogeny, including monocot and eudicot clades. It would be necessary to analyze a less

TABLE 3. Characteristics and numbers of observed β niche (habitat) transitions in island and continental clades estimated by phylogenetic optimization, along with the number expected from a null model.

Clade	Region	Sample/Clade size†	Types of β niche (no. habitats)
Island clades			
<i>Aeonium</i> , <i>Greenovia</i> , and <i>Monanthes</i>	Macaronesia	51/63	cliffs and rocks, xerophytic scrub, thermophile woodland, laurel forest, pine forest, subalpine (6) dry, mesic (2)
<i>Argyranthemum</i>	Macaronesia	51 pops/23 spp.	cliffs and rocks, xerophytic scrub, thermophile woodland, laurel forest, pine forest, subalpine (6) dry, mesic (2)
<i>Echium</i>	Macaronesia	21/27	cliffs and rocks, xerophytic scrub, thermophile woodland, laurel forest, pine forest, subalpine (6) dry, mesic (2)
<i>Sideritis</i>	Macaronesia	32/32	dry, mesic (2)
<i>Sonchus</i>	Macaronesia	31/34	dry, coastal, mesic (3) dry and coastal, mesic (2)
<i>Schiedea</i> and <i>Alsinidendron</i>	Hawaii	30/28	dry forest, dry shrubland, dry cliffs, dry subalpine, shrubland, diverse mesic forest, wescic forest, wet forest (8) dry, mesic (2)
Silversword alliance	Hawaii	36/36	dry, mesic (2)
Continental clades			
<i>Calochortus</i>	Western North America	67/67	serpentine, other habitats (2) forest, open habitats (2)
<i>Narcissus</i>	Europe	23/27	dry rocky open Mediterranean hillsides, montane wet meadows, oak woodland, lowland mesic Mediterranean (4)
<i>Linanthus</i> , Leptosiphon clade	California	28/28	woodland and chaparral, grassy areas, serpentine, desert, drying areas in conifer forest (5) dry, other habitats (2)
<i>Mimulus</i>	Northwestern North America	88/~114	serpentine, other habitats (2) vernal pool, other habitats (2)
<i>Primula</i> sect. <i>Auricula</i>	Alps	25/25	serpentine, other habitats (2) limestone, acid substratum (2) cliffs and rocks, turf, woodland, alpine/subalpine/tundra (4)

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

† Sample/Clade size is the ratio of the no. species (or, in the case of *Argyranthemum*, no. populations) in the phylogenetic analysis to the estimated no. extant species that belong to the clade.

‡ The expected number of transitions shown is the mode of the distribution of 1000 runs of the null model.

§ P values are for the difference between the number of expected transitions and the number of observed transitions (number observed not exceeding number expected).

Sources: 1, Hickman (1993); 2, Baldwin and Robichaux (1995); 3, Wagner et al. (1995); 4, Weller et al. (1995); 5, Bohle et al. (1996); 6, Francisco-Ortega et al. (1996); 7, Kim et al. (1996); 8, Barber et al. (2000); 9, Bell and Patterson (2000); 10, Bramwell and Bramwell (2001); 11, Mort et al. (2002); 12, Beardsley et al. (2004); 13, Graham and Barrett (2004); 14, Patterson and Givnish (2004); 15, Zhang et al. (2004); 16, S. C. H. Barrett, *personal communication*.

rarefied sample if we were asking a solely evolutionary question, but the following question is specific and ecological: “Are specialist members of MG5a communities phylogenetically clustered?” In this case, the method we have used is appropriate and it gives the unequivocal answer, “no.”

It is interesting that Kembel and Hubbell (2006) found an absence of phylogenetic structure in the overall tropical forest community in the 50-ha plot at Barro Colorado Island, but that phylogenetic structure did occur within specific habitats. Our null model and those of Kembel and Hubbell (2006) were different, and this

cannot be ruled out as a source of the opposing results (Gotelli and Graves 1996). It may also be that the much larger species pool for tropical forest ($n = 312$) than for English meadows ($n = 52$) makes phylogenetic structure more likely to occur or easier to detect among specialists.

The approach used to compare niche overlap among congeners with that among other species does not raise phylogenetic sampling issues, but it does assume that α niche dimensions relevant to coexistence have been correctly identified. In each case the dimensions measured do seem likely to fulfil this assumption (Table 2), but as yet very few field studies of putative plant

TABLE 3. Extended.

Observed	No. β niche transitions		Data sources
	Expected \ddagger	P§	
20	25	0.003**	10, 11
10	11	0.303	
21	24	0.071	6
6	10	0.001***	
11	12	0.485	5, 10
5	6	0.272	
13	13	0.681	8
8	11	0.020*	7
6	9	0.036*	
18	21	0.019*	3, 4
6	9	0.020*	
5	8	0.011*	2
10	15	0.011*	14
13	17	0.049*	
8	12	0.003**	13, 16
17	18	0.284	1, 9
6	8	0.092	
3	3	1.000	
3	6	0.002**	1, 12
5	6	0.156	
5	7	0.120	15
12	12	0.641	

niches have proven their role in coexistence beyond all doubt (Silvertown 2004). The result of the congeners test performed here is consistent with large α niche differences that have been found between sympatric species in, among others, the following genera: *Acer* (Sipe and Bazzaz 1994, 1995), *Adenostoma* (Redtfeldt and Davis 1996), *Dryobalanops* (Itoh et al. 2003), *Macaranga* (Davies 2001), *Piper* (Fleming 1985), *Psychotria* (Valladares et al. 2000), *Quercus* (Cavender-Bares et al. 2004), *Ranunculus* (Harper and Sagar 1953), *Salix* (Dawson 1990), and *Typha* (Grace and Wetzel 1981). It is clear that coexisting congeners are often as ecologically different from each other as they are from unrelated members of the same communities. This implies that α niche traits are evolutionarily labile, although proof of this requires evolutionary changes to be analyzed against an explicit, and preferably dated, phylogeny.

Ackerly et al. (2006) tested the order in which α and β niche traits evolved in the shrub genus *Ceanothus*. They

used specific leaf area (SLA) as a proxy measure of the α niche in *Ceanothus* and found that this diverged earlier than their climatically defined measure of the β niche. This finding is at odds with our hypothesis that the α niche is more labile than the β niche (Fig. 1).

β niche transitions

Oceanic islands and island-like habitats, such as vernal pools and serpentine barrens in California, contain multiple radiations that provide replicates for the test of β niche conservatism. There are several examples in the endemic flora of vernal pools in the California Floristic Province (CFP). An extreme case is the monophyletic genus *Downingia* that contains 13 species (Schultheis 2001), all but one of which occur in vernal pools (Ayers 1993). In section *Navarretia* of the genus *Navarretia*, four vernal pool species form a clade that is sister to a species that is facultatively associated with the same habitat (Spencer and Rieseberg 1998). In the much larger genus *Mimulus*, there are roughly six vernal pool species, and four of them are concentrated in one small clade, indicating significant conservatism in this genus, as well (Thompson 1993, Beardsley et al. 2004) (Table 3).

Also in the CFP, significantly conservative evolution of serpentine tolerance is found in the large genus *Calochortus*, where seven of a total of 18 species occurring on serpentine soils belong to a single clade (Patterson and Givnish 2004) (Table 3). Serpentine species in *Mimulus* show slight, though non-significant phylogenetic association (Table 3). Phylogenetic relationships among *Mimulus* species are well resolved, but the weak evidence of phylogenetic conservatism might easily be strengthened by more ecological data. Just three of 28 species in the *Leptosiphon* clade of the genus *Linanthus* occur on serpentine, but they represent three independent evolutionary events (Patterson 1993, Bell and Patterson 2000), so there is no evidence of conservatism in this case.

Kelch and Baldwin (2003) compared the mean genetic divergence measured at ITS and ETS rDNA loci among terminal taxa in seven clades that have evolved within the CFP, in addition to the cases already mentioned. There was a positive relationship between genetic divergence within a clade and the number of plant communities in which its members are found. A clade of *Cirsium* species endemic to the CFP was an outlier from the relationship as a whole, inhabiting a greater variety of plant communities than would be expected for the degree of genetic divergence among its members. This deviation could result either from an abnormally high rate of evolutionary shifts between habitats in the CFP *Cirsium* clade, or an abnormally low rate of molecular evolution. High ecological diversity relative to rDNA variation also occurs in the larger North American *Cirsium* clade of which the CFP endemics form one part (Kelch and Baldwin 2003). This could indicate that the evolutionary lability of habitat depends on lineage.

TABLE 4. Characteristics and no. γ niches, along with no. β niche transitions, based upon upper elevational maximum in two large clades estimated by phylogenetic optimization

Clade	Region	Sample/Clade size	No. γ niches	No. β niche transitions			Data sources
				Observed	Expected	<i>P</i>	
<i>Mimulus</i>	Northwestern North America	88/~114	4	27	27	0.399	2, 3
			2	19	19	0.680	
<i>Pinus</i>	Europe, Asia, North and Central America	101/~120	4	29	37	0.003	1, 4
			2	13	19	0.003	

Notes: Data were analyzed for γ niches coded into four (0–999 m, 1000–1999 m, 2000–3000 m, >3000 m) and two (<2000 m vs. >2001 m) elevational maximum classes (i.e., γ niches). Also see Table 3 footnotes for further explanatory details.

Sources: (1) Mirov 1967, (2) Hickman 1993, (3) Beardsley et al. 2004, (4) Gernandt et al. 2005.

Radiations on islands also show a mixed picture, although conservatism here is more evident than might have been expected given the extreme evolutionary lability of plant form that is present in *Aeonium* (Jorgensen and Olesen 2001), *Sonchus* (Kim et al. 1996), the silversword alliance (Baldwin and Robichaux 1995), and other island endemics. The Hawaiian mints are another endemic group in which considerable morphological variation among species occurs within a restricted range of climatic conditions (Lindqvist et al. 2003). It should be recognized that the crude distinction between wet and dry habitats used for the silverswords in Table 3 does not do justice to the enormous range of soil moisture conditions present in different habitats in Hawaii. The Hawaiian lobelioids are a group that have radiated across the entire soil moisture gradient (Givnish et al. 2004). Nonetheless, the unexpected presence of conservatism of habitat evolution in several island radiations is remarkable. It suggests that speciation often involves interisland colonization between similar habitats (Francisco-Ortega et al. 1996) and that conservative habitat evolution is not confined to continental radiations.

γ niche transitions

The distinction between β and γ niches is not clear-cut, but neither should we expect it to be. The three niche types of α , β , and γ are segments in Hutchinson's (1957) *n*-dimensional hypervolume and are bound to overlap along some dimensions. On some dimensions they may be nested, on others they may not. For example, since elevation and habitat are closely correlated in Macaronesia (Bramwell and Bramwell 2001), conservative evolution of habitat in *Aeonium* and *Sonchus* (Table 3) also implies conservative evolution of elevational distribution. We analyzed elevational maximum in *Mimulus*, where its evolution was not conservative and in *Pinus* where it was (Table 4). Differences in elevational distribution between the pines of different regions of the world were noted by Mirov (1967). Grotkopp et al. (2004) found that species in the subgenus *Pinus* occupied significantly lower elevations than those in subgenus *Strobilus*. This implies that elevational distribution has been conserved since the

two subgenera diverged, which dates it to the deepest node in the phylogeny of *Pinus* (Gernandt et al. 2005). Extant members of the genus comprise a mixture of ancient and quite recently evolved species (Farjon 1996), so conservatism in their elevational distribution cannot simply be attributed to the lack of recent speciation.

Why should α , β , and γ niches evolve with different degrees of lability?

All theories of coexistence based upon nonneutral processes require that species have different α niches in order to coexist (Chesson 2000). Silvertown et al. (2006) argued that, for this reason, community assembly will create structure based upon labile traits. (It will not do so if neutral processes dominate community assembly.) The argument is not that competitive exclusion forces α niches to evolve in a labile manner, but rather that it prevents any traits that might, for whatever reason, not be evolutionarily labile from facilitating coexistence. Nonlabile traits are prevented from defining the α niche by default. Webb et al.'s (2006) study of the effect of interspecific relatedness on seedling mortality implies that apparent competition mediated by disease, as well as direct competition, could cause related species that are insufficiently different to exclude one another at the local scale.

A filtering process might also operate upon the traits that define the β niche, but with opposite effect. Coexisting species must by definition occupy the same habitat and must therefore have β niches that overlap. Thus, the β niche might come to be defined by nonlabile traits.

The filtering processes that could determine the lability of the α niche and the conservatism of the β niche do not as easily explain the conservatism of γ niches, such as the latitudinal ranges of woody plants with disjunct distributions (Qian and Ricklefs 2004). For γ niches, we must invoke either phylogenetic constraint, such as a lack of appropriate genetic variation, or phylogenetic niche conservatism (PNC) (Harvey and Pagel 1991). Although the result of stabilizing selection, it is not clear why PNC should operate with particular effect on the γ niche; we therefore offer a third

explanation. If one thinks of the γ niche as being a geographical area with climatically defined boundaries, then the problem of why it evolves conservatively is closely allied to another evolutionary question: what prevents species at range boundaries from evolving the ability to escape beyond those boundaries? Haldane (1956) proposed the following answer to this question: Adaptation at range boundaries, which is necessary for spread to be possible, might be genetically constrained by the swamping effect of gene flow from individuals in the hinterland that are not adapted to condition at the boundary. This process requires that populations at the periphery of a distribution exist as demographic sinks that require an input of migrants for persistence (Kirkpatrick and Barton 1997, Barton 2001). This is a condition that can be tested.

In this paper we have developed earlier ideas that the hierarchical organization of plant diversity at the α , β , and γ scales proposed by Whittaker (1975) corresponds to a hierarchical set of niches. The traits that define the α niche appear to be evolutionarily labile, whereas the phylogenetic evidence suggests that the β niche evolves in a conservative manner. Perhaps most conservative of all is the γ niche, which is related to geographic distribution. The more conservative a trait, the more remote its origin in evolutionary time and the deeper this lies in a phylogenetic tree. Further exploration of the correspondence between the ecological and evolutionary hierarchies should illuminate our knowledge of both.

ACKNOWLEDGMENTS

J. Silvertown acknowledges the support of a Royal Society travel grant and is grateful to Spencer Barrett and the Botany Department of the University of Toronto for their hospitality during the inception of this paper. We thank Konrad Dolphin, Mike Fay, and Jeffrey Joseph for *rbcL* sequences. D. Gowing and C. Lawson acknowledge the support of Defra and M. Dodd the support of The Open University.

LITERATURE CITED

- Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* **164**:S165–S184.
- Ackerly, D. D. 2004. Adaptation, niche conservatism and convergence: comparative studies of leaf evolution in California chaparral. *American Naturalist* **163**:654–671.
- Ackerly, D. D., D. W. Schwilk, and C. O. Webb. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* **87**:S50–S61.
- Ayers, T. 1993. *Downingia*. Pages 460–462 in J. C. Hickman, editor. *The Jepson manual. Higher plants of California*. University of California Press, Berkeley, California, USA.
- Baldwin, B. G., and R. H. Robichaux. 1995. Historical biogeography and ecology of the Hawaiian silversword alliance (Asteraceae). Pages 259–287 in W. L. Wagner and V. A. Funk, editors. *Hawaiian biogeography*. Smithsonian Institution Press, Washington, D.C., USA.
- Barber, J. C., J. F. Ortega, A. Santos-Guerra, A. Marrero, and R. K. Jansen. 2000. Evolution of endemic *Sideritis* (Lamiaceae) in Macaronesia: insights from a chloroplast DNA restriction site analysis. *Systematic Botany* **25**:633–647.
- Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* **155**:419–434.
- Barton, N. 2001. Adaptation at the edge of a species' range. Pages 3–20 in J. Silvertown and J. Antonovics, editors. *Integrating ecology and evolution in a spatial context*. Blackwell, Oxford, UK.
- Beardsley, P. M., S. E. Schoenig, J. B. Whittall, and R. G. Olmstead. 2004. Patterns of evolution in western North American *Mimulus* (Phrymaceae). *American Journal of Botany* **91**:474–489.
- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* **65**:1406–1419.
- Bell, C. D., and R. W. Patterson. 2000. Molecular phylogeny and biogeography of *Linanthus* (Polemoniaceae). *American Journal of Botany* **87**:1857–1870.
- Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* **57**:717–745.
- Bohle, U. R., H. H. Hilger, and W. F. Martin. 1996. Island colonization and evolution of the insular woody habit in *Echium* L. (Boraginaceae). *Proceedings of the National Academy of Sciences (USA)* **93**:11740–11745.
- Bramwell, D., and Z. Bramwell. 2001. *Wild flowers of the Canary Islands*. Rueda, Madrid, Spain.
- Brummitt, R. K. 1992. *Vascular plant families and genera*. Royal Botanic Gardens, Kew, Surrey, UK. (<http://www.rbkew.org.uk/data/vascplnt.html>)
- Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* **163**:823–843.
- Chazdon, R. L., S. Careaga, C. O. Webb, and O. Vargas. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecological Monographs* **73**:331–348.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**:343–366.
- Clayton, W. D., and H. Williamson. 2003. *World grass flora*. Royal Botanic Gardens, Kew, Surrey, UK. (<http://www.rbkew.org.uk/data/grasses-syn.html>)
- Davies, S. J. 2001. Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology* **82**:920–932.
- Dawson, T. E. 1990. Spatial and physiological overlap of three co-occurring alpine willows. *Functional Ecology* **4**:13–25.
- Ellenberg, H. 1979. Zeigerwerte von Gefässpflanzen Mitteleuropas. *Scripta Geobotanica* **9**:1–122.
- Ellenberg, H., H. E. Weber, R. Düll, V. Wirth, W. Werner, and D. Paulißen. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* **18**:1–248.
- Farjon, A. 1996. Biodiversity of *Pinus* (Pinaceae) in Mexico: Speciation and palaeo-endemism. *Botanical Journal of the Linnean Society* **121**:365–384.
- Fleming, T. H. 1985. Coexistence of five sympatric *Piper* (Piperaceae) species in a tropical dry forest. *Ecology* **66**:688–700.
- Francisco-Ortega, J., R. K. Jansen, and A. Santos-Guerra. 1996. Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora. *Proceedings of the National Academy of Sciences (USA)* **93**:4085–4090.
- Gernandt, D. S., G. G. Lopez, S. O. Garcia, and A. Liston. 2005. Phylogeny and classification of *Pinus*. *Taxon* **54**:29–42.
- Givnish, T. J., R. A. Montgomery, and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany* **91**:228–246.
- Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, D.C., USA.
- Gowing, D. J. G., C. S. Lawson, E. G. Youngs, K. R. Barber, M. V. Prosser, H. Wallace, J. S. Rodwell, J. O. Mountford, and G. Spoor. 2002. The water-regime requirements and the response to hydrological change of grassland plant commu-

- ities. Project BD1310, Final report to DEFRA (Conservation Management Division), London, UK.
- Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist* **118**:463–474.
- Graham, C. H., S. R. Ron, J. C. Santos, C. J. Schneider, and C. Moritz. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* **58**:1781–1793.
- Graham, S. W., and S. C. H. Barrett. 2004. Phylogenetic reconstruction of the evolution of stylar polymorphisms in *Narcissus* (Amaryllidaceae). *American Journal of Botany* **91**:1007–1021.
- Grotkopp, E., M. Rejmanek, M. J. Sanderson, and T. L. Rost. 2004. Evolution of genome size in pines (*Pinus*) and its life-history correlates: supertree analyses. *Evolution* **58**:1705–1729.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**:107–145.
- Haldane, J. B. S. 1956. The relation between density regulation and natural selection. *Proceedings of the Royal Society of London B* **145**:306–308.
- Harper, J. L., and G. R. Sagar. 1953. Some aspects of the ecology of buttercups in permanent grassland. *Proceedings of the British Weed Control Conference* **1**:256–265.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- Hickman, J. C. 1993. *The Jepson manual. Higher plants of California*. University of California Press, Berkeley, California, USA.
- Hill, M. O. 1979. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York, USA.
- Hill, M. O., D. B. Roy, J. O. Mountford, and R. G. H. Bunce. 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *Journal of Applied Ecology* **37**:3–15.
- Hutchinson, G. E. 1957. The multivariate niche. *Cold Spring Harbour Symposia in Quantitative Biology* **22**:415–421.
- Itoh, A., T. Yamakura, T. Ohkubo, M. Kanzaki, P. A. Palmiotto, J. V. LaFrankie, P. S. Ashton, and H. S. Lee. 2003. Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. *Ecological Research* **18**:307–320.
- Jorgensen, T. H., and J. M. Olesen. 2001. Adaptive radiation of island plants: evidence from *Aeonium* (Crassulaceae) of the Canary Islands. *Perspectives in Plant Ecology Evolution and Systematics* **4**:29–42.
- Kelch, D. G., and B. G. Baldwin. 2003. Phylogeny and ecological radiation of New World thistles (*Cirsium*, Cardueae-Compositae) based on ITS and ETS rDNA. *Molecular Ecology* **12**:141–151.
- Kemmel, S. W., and S. P. Hubbell. 2006. The phylogenetic structure of a Neotropical forest tree community. *Ecology* **87**:S86–S99.
- Kim, S. C., D. J. Crawford, J. Francisco-Ortega, and A. Santos-Guerra. 1996. A common origin for woody *Sonchus* and five related genera in the Macaronesian islands—molecular evidence for extensive radiation. *Proceedings of the National Academy of Sciences (USA)* **93**:7743–7748.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. *American Naturalist* **150**:1–23.
- Lindqvist, C., T. J. Motley, J. J. Jeffrey, and V. A. Albert. 2003. Cladogenesis and reticulation in the Hawaiian endemic mints (Lamiaceae). *Cladistics* **19**:480–495.
- Maddison, W. P., and D. R. Maddison. 1992. *MacClade. Analysis of phylogeny and character evolution. Version 3*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Maddison, W. P., and M. Slatkin. 1991. Null models for the number of evolutionary steps in a character on a phylogenetic tree. *Evolution* **45**:1184–1197.
- Mann, L. K., and H. H. Shugart. 1983. Discriminant analysis of some east Tennessee forest herb niches. *Vegetatio* **52**:77–89.
- Mirov, N. T. 1967. *The genus Pinus*. Ronald Press, New York, New York, USA.
- Mort, M. E., D. E. Soltis, P. S. Soltis, J. Francisco-Ortega, and A. Santos-Guerra. 2002. Phylogenetics and evolution of the Macaronesian clade of Crassulaceae inferred from nuclear and chloroplast sequence data. *Systematic Botany* **27**:271–288.
- Nordbakken, J. F. 1996. Plant niches along the water-table gradient on an ombrotrophic mire expanse. *Ecography* **19**:114–121.
- Patterson, R. W. 1993. *Linanthus*. Pages 1037–1046 in J. C. Hickman, editor. *The Jepson manual. Higher plants of California*. University of California Press, Berkeley, California, USA.
- Patterson, T. B., and T. J. Givnish. 2004. Geographic cohesion, chromosomal evolution, parallel adaptive radiations, and consequent floral adaptations in *Calochortus* (Calochortaceae): evidence from a cpDNA phylogeny. *New Phytologist* **161**:253–264.
- Pennington, R. T., Q. C. B. Cronk, and J. A. Richardson. 2004. Introduction and synthesis: plant phylogeny and the origin of major biomes. *Philosophical Transactions of the Royal Society of London B* **359**:1455–1464.
- Pennington, R. T., and C. W. Dick. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Philosophical Transactions of the Royal Society of London B* **359**:1611–1622.
- Pianka, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**:53–74.
- Pickett, S. T. A., and F. A. Bazzaz. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology* **59**:1248–1255.
- Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London B* **268**:2383–2389.
- Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2002. Geographic variability of ecological niches of plant species: Are competition and stress relevant? *Ecography* **25**:721–729.
- Qian, H., and R. E. Ricklefs. 2004. Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. *Journal of Ecology* **92**:253–265.
- Redtfeldt, R. A., and S. D. Davis. 1996. Physiological and morphological evidence of niche segregation between two co-occurring species of *Adenostoma* in California Chaparral. *Ecoscience* **3**:290–296.
- Rodwell, J. S. 1992. *British plant communities. Vol. 3. Grasslands and montane communities*. Cambridge University Press, Cambridge, UK.
- Santos, A. 2001. Flora vascular nativa. Pages 185–192 in J. M. Fernández-Palacios and J. L. M. Esquivel, editors. *Naturaleza de las Islas Canarias*. Turquesa, Santa Cruz de Tenerife, Canary Islands.
- Schaffers, A. P., and K. V. Sykora. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* **11**:225–244.
- Schultheis, L. M. 2001. Systematics of *Downingia* (Campanulaceae) based on molecular sequence data: implications for floral and chromosome evolution. *Systematic Botany* **26**:603–621.
- Shaikat, S. S. 1994. A multivariate analysis of the niches and guild structure of plant populations in a desert landscape. *Pakistan Journal of Botany* **26**:451–465.

- Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology and Evolution* **19**:605–611.
- Silvertown, J., M. Dodd, and D. Gowing. 2001. Phylogeny and the niche structure of meadow plant communities. *Journal of Ecology* **89**:428–435.
- Silvertown, J., M. E. Dodd, D. Gowing, and O. Mountford. 1999. Hydrologically-defined niches reveal a basis for species-richness in plant communities. *Nature* **400**:61–63.
- Silvertown, J., K. McConway, D. Gowing, M. Dodd, M. F. Fay, J. A. Joseph, and K. Dolphin. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society of London B* **273**:39–44.
- Sipe, T. W., and F. A. Bazzaz. 1994. Gap partitioning among maples (*Acer*) in central New England: shoot architecture and photosynthesis. *Ecology* **75**:2318–2332.
- Sipe, T. W., and F. A. Bazzaz. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. *Ecology* **76**:1587–1602.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Fourth edition. W. H. Freeman, San Francisco, California, USA.
- Spencer, S. C., and L. H. Rieseberg. 1998. Evolution of amphibious vernal pool specialist annuals: putative vernal pool adaptive traits in *Navarretia* (Polemoniaceae). Pages 76–85 in C. W. Witham, E. T. Bauder, D. Belk, W. R. Ferren, Jr., and R. Ornduff, editors. *Ecology, conservation, and management of vernal pool ecosystems—proceedings from a 1996 Conference*. California Native Plant Society, Sacramento, California, USA.
- Swofford, D. L. 1996. PAUP*: phylogenetic analysis using parsimony (and other methods). Version 4.0. Sinauer, Sunderland, Massachusetts, USA.
- Sydes, C. L. 1984. A comparative-study of leaf demography in limestone grassland. *Journal of Ecology* **72**:331–345.
- Thompson, D. M. 1993. *Mimulus*. Pages 1037–1046 in J. C. Hickman, editor. *The Jepson manual*. Higher plants of California. University of California Press, Berkeley, California, USA.
- Thompson, K., J. G. Hodgson, J. P. Grime, I. H. Rorison, S. R. Band, and R. E. Spencer. 1993. Ellenberg numbers revisited. *Phytocoenologia* **23**:277–289.
- Tofts, R., and J. Silvertown. 2000. A phylogenetic approach to community assembly from a local species pool. *Proceedings of the Royal Society of London B* **267**:363–370.
- Valladares, F., S. J. Wright, E. Lasso, K. Kitajima, and R. W. Pearcy. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* **81**:1925–1936.
- Wagner, W. L., S. G. Weller, and A. Sakai. 1995. Phylogeny and biogeography in *Schiedea* and *Alsinidendron*. Pages 221–258 in W. L. Wagner and V. A. Funk, editors. *Hawaiian biogeography*. Smithsonian Institution Press, Washington, D.C., USA.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* **156**:145–155.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**:475–505.
- Webb, C. O., G. S. Gilbert, and M. J. Donoghue. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* **87**:S123–S131.
- Weller, S. G., W. L. Wagner, and A. K. Sakai. 1995. A phylogenetic analysis of *Schiedea* and *Alsinidendron* (Caryophyllaceae, alsinoideae)—implications for the evolution of breeding systems. *Systematic Botany* **20**:315–337.
- Whittaker, R. H. 1975. *Communities and ecosystems*. Macmillan, New York, New York, USA.
- Williams, C. B. 1964. *Patterns in the balance of nature and related problems in quantitative ecology*. Academic Press, London, UK.
- Zhang, L. B., H. P. Comes, and J. W. Kadereit. 2004. The temporal course of quaternary diversification in the European high mountain endemic *Primula* sect. *Auricula* (Primulaceae). *International Journal of Plant Sciences* **165**:191–207.