Ecology of plant speciation

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Abstract Ecology affects each of the three principal processes leading to speciation: genetic differentiation among populations within species, acquisition of reproductive isolation among populations, and the rise of ecological differentiation among such populations, allowing them to coexist. Until recently, however, the ties between ecology and speciation in plants have received relatively little attention. This paper reviews some exciting new insights into the role of ecology in speciation, focusing on the angiosperms. I consider five main topics, including (1) the determinants of the spatial scale of genetic differentiation within species; (2) the role and limits of adaptive radiation in increasing net rates of plant diversification; (3) the potential role of ecological speciation; (4) the contributions of hybridization to speciation, adaptive radiation, and the ecological breadth of clades; and (5) the ecological determinants of net diversification rate for individual lineages, and of the species richness for regional floras.

Limited dispersal, especially of seeds, favors genetic differentiation at small spatial scales and is likely to foster rapid speciation and narrow endemism. Meta-analyses show that the minimum area required for in situ speciation on islands increases with the spatial scale of gene flow in various organisms. In angiosperms, fleshy fruits dispersed by vertebrates often increase the distance over which seeds are dispersed, but can decrease it in forest understories. Nutrient-poor soils should work against the evolution of fleshy fruits and promote speciation and narrow endemism.

Selection for adaptation to different conditions drives adaptive radiation, the rise of a diversity of ecological roles and attendant adaptations within a lineage. On islands, adaptive radiation often leads to woodiness, monocarpy, developmental heterophylly, and sexual dimorphism, as well as differences in habitat, growth form, and floral morphology. Adaptive radiation appears to accelerate speciation in only some plant clades. Extensive radiation in some lineages has been ascribed to early colonization, large amounts of heritable genetic variation, "genetic lines of least resistance" upon which selection could act, absence of potential competitors, and possession of "key innovations" that provide access to novel resources. To these should be added large island area, organismal abundance, saturation of ecological space, and the synergism action of limited dispersal and divergent selection producing parallel radiations in isolated regions. Data for Hawaiian lobeliads suggest that within-island species richness of *Cyanea*—involving divergence in elevation and flower tube length—saturates within 0.6 and 1.5 Ma.

Adaptive radiation in pollinators is an important mechanism of ecological speciation: adaptation to different pollinators leads to pollinator partitioning *and* reproductive isolation. Selection for longer nectar spurs and pollinator mouth parts led to increased speciation in *Aquilegia* and other groups. A similar process may work once tubular flowers evolve from cup-shaped blossoms. Selection for floral divergence may be limited in forest understories illuminated by dim, greenish light, which may account for the predominance of small, visually inconspicuous flowers in temperate and tropical understory species.

Hybridization can stimulate speciation by forming transgressive phenotypes that exceed the range seen in parental taxa, and by introgressing adaptive gene combinations. The likelihood of transgressive phenotypes increases with the genetic divergence between parental taxa, so speciation via transgressive hybridization may be most likely among taxa with intermediate amounts of divergence. Several large adaptive radiations appear to have occurred after hybridization, suggesting a special role for the extensive amount of genetic variation that can be supplied and refreshed by syngameons.

Rates of net species diversification are greater in herbs (especially annuals) vs. woody plants; in animal- vs. wind-pollinated species; in plants with poorly dispersed seeds; in families with a greater diversity of growth forms, pollination and seed dispersal mechanisms, and species distributions; in families at lower latitudes; in families with higher rates of genetic evolution; in hermaphroditic or monoecious vs. dioecious clades; in earlier-maturing woody plants; in plants with bilateral vs. radial flowers; in plants with hummingbird-pollinated flowers; in epiphytic vs. terrestrial bromeliads and orchids; in bromeliads differentiating along geographically extensive cordilleras; and in young vs. old clades. Evidence for the last pattern may, however, be an artifact of (auto)regressing $(\ln N) / t$ vs. t. High rates of diversification in epiphytic orchids are tied to small effective population sizes, suggesting a role for intermittent genetic drift alternating with strong selection on floral traits. Across angiosperms, a massive increase in diversification rates was preceded by a major increase in leaf vein density and hydraulic conductance between 140 and 110 Ma ago, leading to higher photosynthetic rates than coexisting ferns and gymnosperms. Based on the economic theory of plant defense, this should have led to lower allocation to anti-herbivore defenses, selecting for low-cost qualitative toxins rather than all-purpose but highly expensive qualitative defenses, triggering an arms' race between angiosperm and their herbivores. Finally, regional plant species richness increases with regional area and proxies for latitude, rainfall, topographic heterogeneity, and vegetation stratification. The Cape Floristic Province has roughly twice as many species as expected from its area and environmental conditions, most likely reflecting the predominance of short-distance dispersal associated with poor soils and myrmecochory in the Cape Province, as well as low rates of regeneration and competitive exclusion following fire.

Keywords adaptive radiation; diversity; genetic structure; seed dispersal; transgressive hybridization

■ INTRODUCTION

Speciation involves three processes: (1) the initial origin of *genetic differentiation* among populations within existing species; (2) the evolution of *reproductive isolation*—that is, the rise of prezygotic and postzygotic barriers to mating between populations, leading ultimately to species formation; and (3) the evolution of *ecological divergence* (ecological isolation sensu Lack, 1971)—that is, the genesis of ecological differences between closely related populations and species that allow them to coexist, permitting long-term persistence of additional new species. Historically, a great deal of emphasis has been placed on the first two processes, involving primarily genetics and the roles of dispersal, population size, breeding system, ploidy, hybridization, and environmental barriers to gene flow in generating genetic differences among populations and incipient mating barriers (Dobzhansky, 1937, 1951; Mayr, 1942, 1963, 1970; Stebbins, 1950, 1971; V. Grant, 1963, 1981; Levin, 2000; D.E. Soltis & al., 2004; P.S. Soltis & Soltis, 2009). In contrast, relatively little of the classic literature on speciation, especially for plants, focused on the role of ecology. Ecological interactions and effects on speciation, for example, occupy no more than a few pages in Verne Grant's (1971, 1981) otherwise magisterial treatments of plant speciation.

Yet the all-pervasive influence of ecology on speciation has long been recognized. Mayr (1947) asserted that isolated populations within species diverged primarily as a result of selection imposed by differences in the environment of such populations; Mayr (1963) later stated "there is hardly an ecological factor that does not affection speciation directly or indirectly, actually or potentially." Verne Grant & Grant (1965) presented a pioneering study of adaptive radiation in floral form and associated pollinators in the phlox family (Polemoniaceae) and inferred that it was a key force driving the divergence of plant species and genera in that group and possibly many others. Carlquist (1970, 1974) argued that adaptive radiation, driven by selection to avoid competition, was a primary driver of plant speciation on islands; Stebbins (1974) made a similar argument for adaptive radiation helping explain the diversification of angiosperms worldwide at the genus and family level. Most recently, Sobel & al. (2010) concluded that essentially *all* mechanisms of speciation—even via polyploidy—are ecological in nature, and downplayed any special significance for Schluter's (1996a) proposed mechanism of ecological speciation.

Although the importance of ecology for speciation has been acknowledged for many decades—arguably, ever since Darwin (1859)—it is only in the last two decades that a decided emphasis has been placed on the ecology of speciation in plants. Only recently have evolutionary biologists begun to explore in detail the specific effects of differences in ecology on plant speciation, and to make specific predications as to how ecological differences might affect speciation and diversification.

Here I review a few of the most exciting advances in our understanding of the relationship of ecology to speciation in angiosperms, focusing on five principal issues:

(1) How do different mechanisms of pollination and seed dispersal affect spatial patterns of genetic differentiation within species, and what might be the implications of such differentiation for speciation?

(2) What are the primary patterns of adaptive radiation in plants? To what extent is adaptive radiation related to increased rates of plant diversification? Why do some lineages undergo extensive radiation and others hardly any? How can limited dispersal and adaptive radiation interact synergistically? Is there evidence that adaptive radiation saturates?

(3) What is the potential role of ecological speciation in plants?

(4) How can hybridization contribute to speciation and extend the ecological range of a lineage, not merely how finely that range is partitioned?

(5) What are the principal ecological determinants of net diversification rates and overall species richness in plants?

■ 1. GENETIC DIFFERENTIATION WITHIN SPECIES AS A FUNCTION OF POLLINATION AND SEED DISPERSAL

Genetic divergence of populations, ecotypic variants, and geographic races within individual species has traditionally been viewed as an important initial step toward speciation in plants (Turesson, 1922; Clausen & al., 1940; Stebbins, 1950; Clausen, 1951; V. Grant, 1956, 1963, 1981; Levin, 2000). Such divergence is critical to the process of allopatric speciation: differences can accumulate, via selection or drift in the absence of gene flow, between isolated sets of populations derived from a single ancestral species, and developmental incompatibilities between genes and genetic backgrounds from sufficiently divergent parents can provide a partial barrier to intermating when populations come back into contact (Dobzhansky, 1937; Mayr, 1942). Such partial barriers, whether pre- or post-mating, should select for reinforcement—that is, for greater pre-mating barriers, so that individuals do not reduce their fitness by mating with members of partly incompatible populations. In time, selection for reinforcement may perfect the mating barriers between divergent populations, completing the process of speciation. Alternatively, such post-contact selection may be swamped by gene flow between hybridizing populations, leading instead to a hybrid complex or homogenization of the initially isolated populations (Liou & Price, 1994; Turelli & al., 2001). Coyne & Orr (1997) elegantly supported the allopatric model of speciation by showing that both pre- and post-mating barriers increase with genetic distance among species and populations of *Drosophila*, and that pre-mating barriers evolve more rapidly between sympatric taxa. These patterns recur in several other animal groups (Coyne & Orr, 2004), and reinforcement in sympatric plant species has been demonstrated for *Gilia* (V. Grant, 1966), *Phlox* (Levin & Kerster, 1967), and *Costus* (Kay & Schemske, 2003).

Reduction in gene flow between populations is critical for all models of speciation, including not only allopatric speciation, but also **parapatric and sympatric speciation** (Liou & Price, 1994; Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2003; Heinz & al., 2009), **runaway sexual selection**

(Day, 2000), **polyploidy/chromosomal evolution** (Ramsay & Schemske, 1998, 2002; Rieseberg, 2000; Navarro & Barton, 2003), **selection for assortative mating** (S.D. Johnson & al., 2006), and **ecological speciation** (Schluter, 2000; Rundle & Nosil, 2005; Peccoud & Simon, 2010). Reduced gene flow should make speciation more likely, just as it makes genetic differentiation along spatial gradients more likely (Slatkin, 1973, 1985; Endler, 1977; Doebeli & Dieckmann, 2003). Although current and historic patterns of gene flow are difficult to separate, both are reflected in present-day patterns of genetic structure within populations.

Research over the past few decades has cast considerable light on the amount of genetic variation within and among populations of individual plant species, the spatial scales over which genetic differentiation occurs, and the biological/ecological correlates of such differentiation. Extensive reviews of allozyme diversity by Loveless & Hamrick (1984) and Hamrick & Godt (1989, 1996) showed that these codominant markers showed relatively more differentiation among vs. within populations (i.e., had higher values of G_{ST}) in selfers vs. outcrossers, in hermaphroditic vs. monoecious or dioecious species, in sexual vs. asexual taxa, in gravity-, animal-, and explosive dehiscence-dispersed vs. wind-dispersed taxa, in short- vs. tall-statured plants, and in widespread vs. narrowly distributed species. Hamrick & Godt (1996) found significantly higher values of G_{ST} in species with ingested fleshy fruits or gravity-dispersed seeds than in species with wind dispersal or ectozoochorous propagules dispersed on the outsides of animals. They also showed that the greatest proportion of variation in G_{ST} was explained by the combinations of breeding system with seed-dispersal mode and taxonomic status (dicots vs. monocots vs. gymnosperms), and that woody plants had substantially lower values of G_{ST} than herbs with the same life-history traits. Based on these data, we would expect that speciation rates should be highest in selfers, hermaphroditic taxa, sexual species, gravity- and fleshy-fruited taxa, herbs, and widespread taxa.

It should be noted, however, that interpreting these data has several difficulties, including (1) separating the effects of multiple species traits that are also correlated with each other; (2) the lack of phylogenetic independence of the taxa and traits considered as independent units by Hamrick, Loveless, and Godt; (3) the lack of data on the physical distances among populations for each species; (4) derivation of all allozymes from the nuclear genome, with none from the plastid or mitochondrial genomes; and (5) lack of data with which to estimate the relative amounts of gene flow via pollen vs. seeds.

Duminil & al. (2007) attempted to address the first two issues by using phylogenetically independent contrasts (PICs: Felsenstein, 1985) to control for evolutionary relationships among the taxa they included, and partial regressions on PICs to assess the independent effects of each life-history traits considered. Separate analyses were conducted for maternally and biparentally inherited DNA markers. Almost all of the correlations found by earlier analyses of isozyme data disappeared in this study; only correlations of G_{ST} with geographic range size, selfing vs. outcrossing, and gravity-dispersed seeds vs. all other

dispersal mechanisms remained. Duminil & al. (2007) found that nearly 80% of the variation in G_{ST} is accounted for a species' taxonomic position at the ordinal level and below. The authors cast their surprising results as an example of "the highly contingent nature of evolution", concluding that "predicting the fate of species … on the basis of simple traits is rarely possible." Before we accept their rather nihilistic conclusion, however, this analysis must be reconsidered and substantially extended. The inference by Duminil & al. (2007) that ca. 80% of the variation in G_{ST} is related to taxonomic affinity may simply be a testimony to the strong tie of various life-history traits (and their combinations) to particular orders, families, and genera in a limited dataset. While such a sampling artifact would result in categorizing most ecological effects as taxonomic effects instead, such a sampling artifact should disappear if a wider range of taxa were included—including several "replicate," distantly related groups at various levels with the same or similar life-history characteristics—and a more reliable estimate of ecological effects captured. Careful attention to taxon sampling is critical to all comparative studies (Ackerly, 2000). Future extensions of the Duminil & al. study should use the more powerful tests of correlated evolution now available (e.g., Pagel, 1999; Pagel & Meade, 2006). Problems with correlated evolution of phylogenetically conservative character-states that are also tied to particular ecological conditions and life-history traits will, however, likely remain quite difficult (Ricklefs & Stark, 1996).

Studies that relate multi-locus measures of genetic divergence to distance between pairs of individuals (or populations) to infer the spatial scale of genetic differentiation and gene flow are still in their infancy (Smouse & Peakall, 1999; Rousset, 2000; Vekemans & Hardy, 2004; Hardy & al., 2006; Grivet & al., 2009). Vekemans & Hardy (2004) advocated the Sp statistic—essentially, the rate of decline in genetic identity with the logarithm of distance, over the range where both are linearly related—as the preferred measure of the spatial scale of genetic differentiation. They found differentiation at significantly smaller spatial scales in selfing vs. outcrossing and self-incompatible species, and in herbs vs. woody plants. Their data also imply differentiation at smaller scales in woody species with gravity vs. animal dispersal of seeds ($P < 0.036$ for 2-tailed t-test, 12 d.f.). These measurements are, however, few in number compared with the allozyme data, so conclusions based on them are necessarily tentative. Several groups—notably, understory rain-forest trees and shrubs with fleshy fruits, an enormously diverse group in many areas of the Neotropics (Gentry, 1982; Givnish, 1999)—remain essentially unsampled.

Petit & al. (2005) found that, across 183 species of angiosperms, G_{ST} is much higher for maternally inherited organeller markers (median = 0.67) than for nuclear markers (median = 0.10). They also claimed that, at a range-wide level, pollen accounted for roughly ten times as much gene flow as did seeds. A number of other recent studies have similarly asserted that the distance of pollen flow greatly exceeds that via seed movement (e.g., Burczyk & al., 2006; Bittencourt & Sebbenn, 2007; Nakanishi & al., 2009), though some papers (e.g., Bacles & al., 2006; Hardesty & al., 2006) report contrary findings.

However, Grivet & al. (2009) provide a compelling analysis—based on data from seven microsatellite loci in a population of California valley oak (*Quercus lobata*), sampled from adults and from seedlings with both maternal and biparental tissue attached, and analyzed using a parent-offspring correlation model—that shows that even in this wind-pollinated species, dispersal of its heavy, scatter-hoarded seeds dominates the determination of the spatial scale of genetic differentiation. Effective population sizes for maternal parents were only 1.1 to 2.7 plants, vs. 8.1 to 15.4 for paternal parents, leading to overall effective population sizes of 3.6 to 6.7 trees. This corresponds to a root-mean-square distance σ of overall gene flow of a few tens of meters, vs. an estimated pollen s of 60 to 350 m (Grivet & al., 2009; Pluess & al., 2009). A similar study, involving SSR variation in pedunculate oak (*Q. robur*) from Bordeaux, showed that significant fine-scale genetic structure occurs over scales <30 m (Hampe & al., 2010). While long-distance pollen movement also occurs in this species, short-distance seed movement from only a few trees favored by jays that disperse acorns results in local genetic structure being passed from one generation to the next.

Voigt & al. (2009) used kinship analysis to infer gene flow distances in two fleshy-fruited species of *Commiphora* (Burseraceae). *Commiphora harveyi*, native to South Africa, is visited by at least ten bird species which—based on direct observations—move the seeds roughly 65 m from maternal trees. *Commiphora guillauminii*, native to Madagascar, is visited by a single bird species, which moves the seeds less than 1 m. Kinship analysis showed genetic differentiation (and, by implication, total gene flow) over scales <3 km in Madagascar, and <30 km in South Africa (Voigt & al., 2009). Krauss & al. (2009) found a median seed dispersal distance of 5 m in *Banksia hookeriana* (Proteaceae) in southwest Australia. This corresponded, as expected, to a peak in spatial genetic autocorrelation between 0 and 5 m, despite the fact that pollen movement by nectivorous birds was essentially random over far greater distances—involving more than twice as many paternal parents as the 70 m × 80 m study area. These studies demonstrate that seed dispersal can be a decisive determinant of overall gene flow. This conclusion is reinforced by the facts that (1) seeds carry twice as much genetic information as pollen, and—as is often overlooked—(2) genetic structure created by a species invading new territory can only be generated, at least initially, by seed dispersal.

Speciation in relation to the scale of intraspecific gene flow

In general, the likelihood of speciation occurring within a region should increase with the size of that region and decrease with the spatial extent of intraspecific gene flow. Kisel & Barraclough (2010) provide evidence supporting these predictions from meta-analyses of population genetic studies and the minimum areas of oceanic islands associated with speciation in bats, carnivorous mammals, birds, flowering plants, lizards, and snails (Fig. 1). Only ferns fail to show a significant relationship of the chance of speciation to island area, presumably

because they often speciate via the scale-independent processes of polyploidy and/or hybridization (Kisel & Barraclough, 2010). Flowering plants, in this pioneering study, emerge as having quite low minimum distances of gene flow, comparable to land snails, and speciating at correspondingly small scales. As studies of the spatial scale of genetic differentiation in plants proliferate, applying this kind of analysis within the angiosperms should provide a powerful test of the importance of different dispersal mechanisms in determining the geographic pattern of genetic variation within species and the subsequent likelihood of speciation. The advantage of short-distance seed dispersal for speciation must be set against the increased likelihood of extinction of narrowly distributed taxa (see Givnish & al., 1995).

Fleshy fruits in understory species. — One especially interesting prediction to pursue is that fleshy fruits in tropical moist and wet forest understories should result in quite limited seed dispersal—and thus, in extensive speciation—as a consequence of the sedentary nature of understory birds that consume such fruits (Givnish & al., 1995, 2009; Givnish, 1998, 1999; see also Price & Wagner, 2004). At present, there are far too few published accounts of genetic structure in such plants to come to any conclusions (but see Loiselle & al., 1995; Theim, 2008). However, Burney & Brumfield (2009) recently documented patterns of differentiation across major barriers in South America (Andes, Amazon, Rio Madeira) in 40 bird species occupying different forest strata; several groups of facultative and obligate frugivores were represented. They showed that, as argued by Diamond & al. (1976), birds from lower forest strata are progressively more sedentary. In fact, foraging stratum had, by far, the strongest effect on genetic isolation by distance within species across all three biogeographic barriers. Moore & al. (2008) used experimental releases to show that six of the ten most common understory birds around Lake Gatun
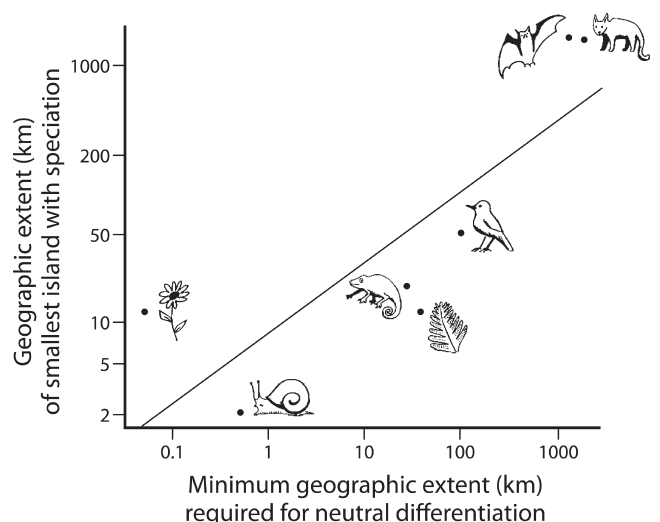

Fig. 1. Minimum island area required for in situ speciation for various groups of organisms vs. the physical distance required for neutral genetic differentiation (*Nm* = 1). Data based on meta-analysis of speciation on 64 island groups, as well as a meta-analysis of gene flow data largely drawn from Morjan & Rieseberg (2004). Redrawn from Kisel & Barraclough (2010).

in Panama could not disperse over water gaps of 300 m or less; one species (*Myrmotherula fulviventris*) never dispersed over even 100 m of open water. Dispersal ability measured this way correlated well with species occurrence on lake islands isolated from occupied islands by different distances.

Several ecologists have argued that rain-forest canopies show much greater horizontal variation in environmental conditions due to large treefall gaps than does the shaded understory below continuous canopies (Terborgh, 1980; Terborgh & al., 1990; Richards, 1996). As a consequence, such species tend to occur across a wider range of habitat types (Terborgh & Weske, 1969; Pearson, 1971; Terborgh, 1980; Walther, 2002) and have a greater propensity for dispersal than understory species (Fogden, 1972; Terborgh, 1980, 1986; Loiselle, 1988; Levey & Stiles, 1994). Diamond (1973), Diamond & al. (1976), and Yumoto (1999) argued that understory birds, compared with those of gaps or the canopy, are especially loathe to cross water barriers; they ascribed the greater tendency toward speciation in understory birds to such limited dispersal ability. Burney & Brumfield (2009) found that understory species had a higher value of Kipp's index ($I_k = 100 \times DS1 / W$, where $DS1$ is the distance from the first secondary to the wing tip when the wing is folded, and W is the length of the folded wing) than canopy birds, providing further support for understory species having low dispersal capacity. The authors also found that understory species had the expected greater tendency to form recognized subspecies.

Givnish & al. (1995, 2009) ascribed the much greater number of species in the endemic Hawaiian genus *Cyanea* (ca. 76) than in its sister *Clermontia* (22 spp.) to the fact that *Cyanea* mainly occupies continuous, densely shaded forest understories in Hawaii, while *Clermontia* primarily lives in gaps and edges of the same forests. Both genera bear fleshy fruits and exhibit the same ranges in elevation and floral tube length; the latter, presumably, reflects the bill length of the honeycreepers and other birds that formerly pollinated individual species. As expected, individual species of *Cyanea* have narrower elevational and geographic ranges than those of *Clermontia*; each species of *Cyanea* occurs almost exclusively on a single island in the Hawaiian chain. A greater tendency toward speciation in fleshy-fruited plants of tropical forest understories appears to be a general tendency. Ten of the twelve largest genera in the Hawaiian flora are fleshy-fruited plants of shaded forest understories (Givnish, 1998: $P < 0.020$, 1-tailed exact test); seven of the eleven largest Hawaiian plant clades are bird-dispersed elements of wet-forest understories (Price & Wagner, 2004; $P < 0.029$, 1-tailed exact test). Avian dispersal (including ectozoochory) is the strongest correlate of species number across 28 Hawaiian plant clades (Price & Wagner, 2004). In a survey of Neotropical understory clades with fleshy fruits, J.F. Smith (2001) found that 11 of 14 had more species than the dry-fruited clades to which each was sister. Many of the largest angiosperm genera (e.g., *Chamaedorea*, *Geonoma*, *Piper*, *Psychotria*, *Solanum*) are composed mainly of tropical forest understory shrubs and trees with fleshy fruits (Givnish, 1998, 1999). These findings run counter to previous inferences that there is no significant positive relationship between fleshy fruits and species

richness (Herrera, 1989; Fleming, 1991; Midgely & Bond, 1991; Ricklefs & Renner, 1994). However, these studies made no distinction between endozoochory in forest understories vs. gaps or canopies. In the latter ecological context, fleshy fruits should provide excellent dispersal over moderate to long distances, and so show a *negative* association with species number. Pooling clades with fleshy fruits from understory, gap, and canopy environments is thus likely to produce little or no expected difference in speciation and net diversification compared with other dispersal mechanisms—as observed.

Plants with fleshy fruits make up a greater fraction of the flora of rainier forests in the Neotropics (Gentry, 1982, 1988), and on taller islands receiving more rainfall (Carlquist, 1974). Furthermore, endozoochory in Neotropical forests is more common among taxa fruiting in the rainy season than in those fruiting in the dry season (Smythe, 1970; Croat, 1978). Heavy rainfall might promote the evolution of fleshy fruits in three ways, by (1) working against wind dispersal, which is relatively more effective during dry, often windy conditions (Smythe, 1970; Gentry, 1982); (2) favoring additional stems or strata in the windless understory, by decreasing root allocation and, therefore, increasing shade tolerance (Givnish, 1999); and (3) helping produce abundant flushes of new, soft foliage (Frankie & al., 1974) that is especially vulnerable to caterpillars (Coley, 1983), thus providing a "protein subsidy" to the many frugivorous birds that supplement their diet by gleaning insects from foliage (see Givnish, 1998). All three of these mechanisms, plus a potentially stronger operation of density-dependent mortality imposed by specialist herbivores in rainier habitats, could help accelerate speciation in wet tropical forest understories and help account for the observed increase in woody plant richness with increasing rainfall in the Neotropics (Givnish, 1999). Vertebrates consuming fleshy fruits are far more likely to disperse seeds over long distances (at least outside forest understories) than ants carrying seeds with elaiosomes; mean dispersal distances for myrmecochorous seeds are typically of order 1 m across habitats (Gomez & Espadaler, 1998).

Soil infertility as a contributor to narrow endemism. — The importance of a frugivore protein subsidy for plant speciation should be explored in other contexts. Specifically, plants on nutrient-poor soils should heavily defend their leaves to maximize growth and survival (Janzen, 1974; Coley, 1983), which in turn should greatly reduce such a protein subsidy and, with it, overall frugivore abundance (Givnish, 1998). Increased reliance on wind or gravity dispersal on such sterile substrates, especially in open habitats, should increase speciation and narrow endemism in plants. Poor soils, together with seasonal aridity, might help account for the low incidence of fleshy fruits in the open South African fynbos. I propose that limited seed dispersal, based on a resulting reliance on gravity, wind, or ants to transport propagules, could be one of several factors promoting high rates of speciation in that community (see also Bond & Slingsby, 1983; Linder, 1985, 2005, 2008). Soil infertility, by reducing the incidence of taxa with fleshy fruits even in hyperhumid areas like the sandstone tepuis of South America, may also help generate high rates of speciation and local endemism there (Givnish, 1998).

■ 2. DIVERSIFYING INFLUENCE OF ADAPTIVE RADIATION

Adaptive radiation—the rise of a diversity of ecological roles and attendant adaptations within a lineage—is arguably one of the most important processes bridging ecology and evolution (Lack, 1947; Carlquist, 1970, 1974; Givnish, 1997; Schluter, 2000; Linder, 2008; Gavrilets & Losos, 2009). It arises as a result of divergent selection within species or among closely related taxa for adaptation to different environments, resources, competitors, predators, and/or mutualists. Such selection can arise as a result of an ancestral species invading a new or remote area (e.g., an oceanic island, a lake, or a mountaintop) largely devoid of other species, the extinction of previously dominant groups, or the rise of a "key innovation" (e.g., the tank habit in bromeliads) that allows the invasion of a new "adaptive zone" (e.g., epiphytic perches atop other plants) (Simpson, 1953). Competition within an ancestral species should become intense as it becomes more common, leading to selection for variants that use alternative environments or resources. When the products of such divergence come into secondary contact, if they have not already diverged sufficiently to avoid most competition, there should be selection for members of such populations to diverge further ecologically, and thus acquire the *ecological differentiation* required for their local long-term coexistence. If breeding barriers have not already been perfected, there should also be selection for reinforcement and acquisition of *reproductive isolation* between such populations to prevent interbreeding. Over time, there should be selection for additional ecological and reproductive isolation among newer members of the radiation. In many cases, at least initially, this might lead to ecological or reproductive *character displacement*, in which closely related, ecologically similar species are more divergent from each other in sympatry than in allopatry (Brown & Wilson, 1956; P.R. Grant, 1972; Schluter & MacPhail, 1992).

Adaptive radiation can thus be a major source of ecological diversity and new taxa. For example, in the native Hawaiian flora, the 20 largest clades—all but one of which involve extensive adaptive radiation in habitat, pollination biology, and/or vegetative form—generated more than half of the native species from only 7.6% of the initial colonists that left descendants (see section below on Adaptive radiation and speciation). Underutilized resources provide a mechanism for generating ecological isolation between species, acting at the same time as sexual selection for reproductive isolation (see section on Ecological speciation) or subsequently. Selection for adaptation to different environments and resources can result not only in remarkable cases of divergence within radiations, but also convergence between ecologically similar members of different radiations, as illustrated by marsupial vs. placental mammals, Hawaiian honeycreepers vs. other families of passerine birds (and perhaps other vertebrates—Lovette & al., 2002), cichlids in different African rift lakes, the rise of trees from several herbaceous plant lineages colonizing islands, and the repeated origin of unscented, tubular, reddish flowers with copious nectar in unrelated plants pollinated by hummingbirds. Extensive

divergence and convergence within radiations on islands can confound attempts to infer ancestral mainland taxa and trace patterns of adaptive evolution using phylogenies based on morphology, making phylogenetic analysis based on molecular data crucial for the analysis of such radiations (Givnish & al., 1994, 1995, 1997; Sang & al., 1994; Baldwin & Robichaux, 1995; Böhle & al., 1996; Kim & al., 1996; Francisco-Ortega & al., 1997).

Patterns of adaptive radiation

Adaptive radiation provides some of the most spectacular illustrations of the ties between ecology and evolution in plants. Notable instances on individual oceanic islands or archipelagoes include:

(1) **Hawaiian lobeliads** (128 spp. of treelets, trees, shrubs, woody rosettes, and vines, ranging from mesic to wet scrub and forests to subalpine bogs and seacliffs, bearing highly divergent leaves, flowers and fruits, diverged from other woody lobeliads from Africa and other islands in the Pacific 13 million years (Ma) ago [Givnish & al., 1994, 1995, 2009]);

(2) **Hawaiian silversword alliance** (25 spp. of shrubs, trees, and woody vines, ranging from very dry to very wet habitats, derived from herbaceous California tarweeds 5.2 Ma ago [Carlquist, 1970; Robichaux & al., 1990; Baldwin & al., 1991; Baldwin & Sanderson, 1998; Carlquist & al., 2003]);

(3) **Hawaiian *Schiedea*** (34 spp. of herbs, shrubs, and vines, ranging from dry cliffs to wet forests and varying from hermaphroditic to dioecious, apparently divergent from circumboreal *Honckenya* and *Wilhelmsia* [P.S. Soltis & al., 1996; Wagner & al., 2005b; Sakai & al., 2006; Weller & al., 2006; Harbaugh & al., 2010]);

(4) **Hawaiian *Chamaesyce*** (15 spp. of sprawling mats, shrubs, and trees, from coastal vegetation to wet forest, with an extraordinary range in leaf venation patterns and stomatal distributions [Carlquist, 1970; Sporck & Sack, in prep.);

(5) **Macaronesian *Aeonium* alliance** (61 spp. of annual and perennial herbs, subshrubs, rosettes, succulents, each possessing the C_3, CAM, or C_3-CAM photosynthetic pathway, and derived from northwest African herbaceous ancestors 18.8 Ma ago [Mes & t'Hart, 1996; Jorgensen & Oleson, 2001; Mort & al., 2002, 2007; Kim & al., 2008]);

(6) **Macaronesian *Echium*** (28 spp. of shrubs, trees, and secondarily derived annual herbs from a very wide range of rainfalls and elevations, and having diverged from mainland herbaceous *Echium* 7.9 Ma ago, colonizing the Canary Islands first, and then diversifying on Madeira and the Cape Verde Islands [Böhle & al., 1996; Kim & al., 2008; Gárcia-Maroto & al., 2009]);

(7) **Macaronesian *Sonchus* alliance** (31 spp. of tuberous herbs and woody subshrubs, shrubs, and rosette trees, ranging from dry to mesic habitats, and having diverged from mainland herbaceous ancestors 13.2 Ma ago [Kim & al., 1996, 2008; Lee & al., 2005]);

(8) **Macaronesian *Argyranthemum*** (24 spp. of woody perennials that vary substantially in leaf division and range from dry to mesic habitats [Francisco-Ortega & al., 1996, 1997]; and

(9) **New Zealand *Hebe* complex** (124 spp. with extraordinary variation in growth form, leaf shape, and habitat [Garnock-Jones, 1993; Albach & al., 2004, 2005]).

There are many other striking cases of insular radiation in plants (e.g., *Araucaria, Bidens, Crambe, Cyrtandra, Geranium, Hibiscadelphus, Melicope, Myrsine, Phyllostegia, Stenogyne, Pericallis, Pittosporum, Pouteria, Psychotria, Robinsonia, Scaevola, Sideritis*), and several on continents (e.g., *Acacia, Banksia*, and *Eucalyptus* in Australia; *Disa, Erica, Gladiolus, Moraea*, and families Aizoaceae and Restionaceae in South Africa; *Brocchinia, Calceolaria, Espeletia, Fuchsia, Lepanthus, Lupinus* and families Bignoniaceae, Bromeliaceae, and Rapateaceae in South America; and *Aquilegia, Calochortus, Lilium, Mimulus, Penstemon, Platanthera, Quercus, Trillium*, and the family Polemoniaceae in North America). Continental lineages, by virtue of having access to a much wider range of parent material than lineages on volcanic islands, often show adaptive radiation by soil type or bedrock (e.g., invasion of serpentine, gypsum, alkali, clay, loamy, and sandy soils by *Calchortus*; invasion of serpentine and vernal pools by *Navarretia*). In California, with extensive outcrops of serpentine, ca. 215 species have become specialized entirely to serpentine soils; in the limited number of closely related species found on serpentine and non-serpentine, growth and survival on one substrate was inversely related to that on the other (Kruckeberg, 1951; Brady & al., 2005).

Each of the nine island groups highlighted above fit the criteria for adaptive radiation given by Givnish (1997): each is monophyletic, each encompasses substantial ecological diversity, and each exhibits evidence—most often, in terms of comparative data showing a regular fit between form and morphology (e.g., of leaf width to moisture supply)—that supports differential adaptation of individual species to different conditions. In addition to these criteria, Schluter (2000) emphasized two others: *rapid speciation* and *experimental evidence of a trait-utility connection*. Rapid speciation is problematic as a defining criterion of adaptive radiation (see Givnish, 1997), although all of the cases listed above fit in the time frame of other radiations mentioned by Schluter (2000). No study, to my knowledge, has ever defined "rapid speciation," and no study has ever excluded a lineage as being an adaptive radiation on this basis; the rapid-speciation criterion is simply not operational. Givnish (1997: table 1 and pp. 17–21) also identified experimental evidence of different utilities for traits in different environments as being highly desirable. To show that a radiation is adaptive, one *must* present evidence based on comparative data, functional studies, or direct measurements of fitness that variation in the underlying traits increases fitness in the conditions occupied and not in others. However, it is not clear why Schluter (2000) insisted on evidence of differential utility from comparative and functional studies, but not from direct measurements of fitness; all three approaches can provide evidence of differential utility (Givnish, 1997). Given that divergent members of many adaptive radiations inhabit and thus develop in different environments, we should also insist on using common gardens/zoos to demonstrate that differences in trait expression and utility among members of a radiation in different environments are

at least partly genetic and not wholly a result of developmental plasticity and the different conditions under which different species develop (Baldwin, 1997; Givnish, 1997). To date, unfortunately, such common-garden studies of adaptive radiation in plants have been rare for trait expression (e.g., Baldwin, 1997) and especially for trait utility, but several studies of the latter have recently appeared (Schemske & Bradshaw, 1999; Givnish & al., 2004; Verboom & al., 2004; Angert & Schemske, 2005; Muchhala, 2007; Schemske & Bierzychudek, 2007; Angert & al., 2008; Montgomery & al., 2008).

A lineage with few (but two or more!) species could still be considered an adaptive radiation if the extent of divergence among its species in ecology within or between habitats would typically be regarded as adequate to permit long-term coexistence of those species. Excluded would be cases of *non-adaptive radiation* (see Gittenberger, 1991; Cameron & al., 1996; Givnish, 1997; Rundell & Price, 2009). Allopatric speciation resulting from geographic barriers or limited dispersal can easily result in non-adaptive radiation, or speciation without ecological divergence and the rise of corresponding adaptations, as occurs often in groups of burrowing mammals (e.g., gophers, mole rats), land snails, and brooding Antarctic sea urchins. The bromeliad genus *Navia* (see below) provides a potential example in plants.

Common ecological trends in plant radiations on islands include the evolution of woodiness, monocarpy, developmental heterophylly, and sexual dimorphism, as well as the rise of differences in growth form, habitat, and floral morphology (Carlquist, 1965; Givnish & al., 1994, 1995; Weller & al., 1995, 1998; Böhle & al., 1996; Givnish, 1998; Jorgenson & Olesen, 2001; Sakai & al., 2006). In an attempt to determine the nature of phenotypic shifts within insular radiations without having access to actual phylogenies, Jorgensen & Olesen (2001) tallied the proportion of dichotomies involving vegetative, floral, or fruit characters in the published keys to all native genera with ≥10 species present in the Hawaiian and Canary Islands. For Hawaiian taxa, 45% of dichotomies within genera were floral, vs. 42% for vegetative characters and 13% for fruit characters. The genera pollinated by birds had the six highest fractions of dichotomies involving floral characters, ranging from 92% in *Clermontia* to 53% in *Cyanea* and averaging 66% overall, compared with 36% for the genera pollinated by other animal groups. No leading Canarian genera are pollinated by birds; floral dichotomies for them averaged 36% as well. Verne Grant (1949), in a survey of angiosperm groups slanted more to temperate mainland areas, found that the proportion of floral diagnostic characters was roughly 40% for plants with specialized animal pollinators; 15% for those with promiscuous insect pollinators; and 4% for wind-pollinated taxa. These data imply that selection for floral divergence is strongest in plants visited by specialized pollinators, weaker in those visited by unspecialized pollinators, and weakest in wind-pollinated plants. Furthermore, animal pollination is generally associated with higher rates of diversification than wind pollination (Kay & al., 2006). Based on comparisons of sister clades, one wind-pollinated and the other animal-pollinated, 11 of 16 cases had more species associated with animal pollination ($P < 0.033$ for

various statistical tests advanced by the authors). At a broader level, 202 of 379 families were characterized by biotic pollination vs. 39 by wind or water pollination.

Schiestl & Schlüter (2009) provide the only study relating the degree of floral specialization to plant speciation. Phylogenetically structured comparisons of floral and pollinator differences among species within 27 orchid genera showed that the number of species per genus was inversely related to the number of pollinators per species (Fig. 2). That is, orchid genera that had species that were more specialized on individual pollinators were more likely to undergo extensive speciation or, more precisely, a greater excess of speciation over extinction. More pollinators were shared by species within genera involving the presentation of real or deceptive food rewards than in genera employing sexual deception (i.e., pseudocopulation and dummy brood sites) or scent rewards (e.g., essential oils) used by pollinators for their own reproduction. These data support Dressler's (1981) argument that orchid pollinators should be more faithful—and provide better reproductive isolation to the plants they visit—if they respond to sexual deception or scent rewards, because such responses are directly connected to sexual selection and reproductive barriers operating on the pollinators themselves.

Van der Niet & Johnson (2009) provide the most compelling summary to date of the nature of ecological shifts within adaptive radiations in a mainland area. They tallied differences between species for 188 pairs of sister taxa drawn from phylogenies for eight major lineages native to the Cape floristic region in South Africa, including *Disa* (Orchidaceae), Heliophileae (Brassicaceae), *Muraltia* (Polygalaceae), *Pelargonium* (Geraniaceae), Podalyrieae (Fabaceae), the *Restio* clade (Restionaceae), and *Satyrium* (Orchidaceae). The Cape floristic region

comprises one of the world's six floral kingdoms (Takhtajan, 1986) and is a major biodiversity hotspot, with ca. 9000 species in an area of 90,000 km^2, and local endemism approaching 70% (Goldblatt & Manning, 2002), and numerous plant radiations, many prominently including specialization on various classes of pollinators (Linder, 2003, 2005, 2008; S.D. Johnson, 2010). Van der Niet & Johnson (2009) found that, in terms of ecology, complete shifts in pollinators (33% of Cape sister species pairs), fire survival strategies (33%) and general habitat excluding shifts in soil type (32%) were the most frequent observed, while shifts in soil type were the least frequent, with 17% of species pairs exhibiting complete shifts and 28% partial shifts. For species pairs exhibiting only one ecological shift, 53% showed a shift in flowering time, while none showed a shift in soil type. Most sister species pairs in both animal- and wind-pollinated lineages exhibited shifts in both floral and vegetative traits. Overall 33% of Cape species pairs had allopatric ranges, 10% were wholly sympatric, and 57% overlapped in part, supporting allopatric or parapatric speciation as a dominant force. The relatively high frequency of species shifts in habitat, elevation, and geographic ranges is expected from theory, based on the greater ease of reproductive and adaptive divergence evolving when they are tied to spatially limited areas (see Gavrilets, 2004; Gavrilets & Vose, 2005, 2009; Gavrilets & Losos, 2009; Ravigné & al., 2009). Verne Grant (1949) believed that the first step of many adaptive radiations in flowering plants involved pollinator shifts (see also Schluter, 2000), but the preponderance of evidence from the preceding analysis of Cape plant lineages, the patterns of divergence in distribution vs. flowers in *Calochortus* (Patterson & Givnish, 2004), and the patterns of divergence in habitat, growth form, elevation, and flower tube length in Hawaiian lobeliads (Givnish & al., 1995, 2009)
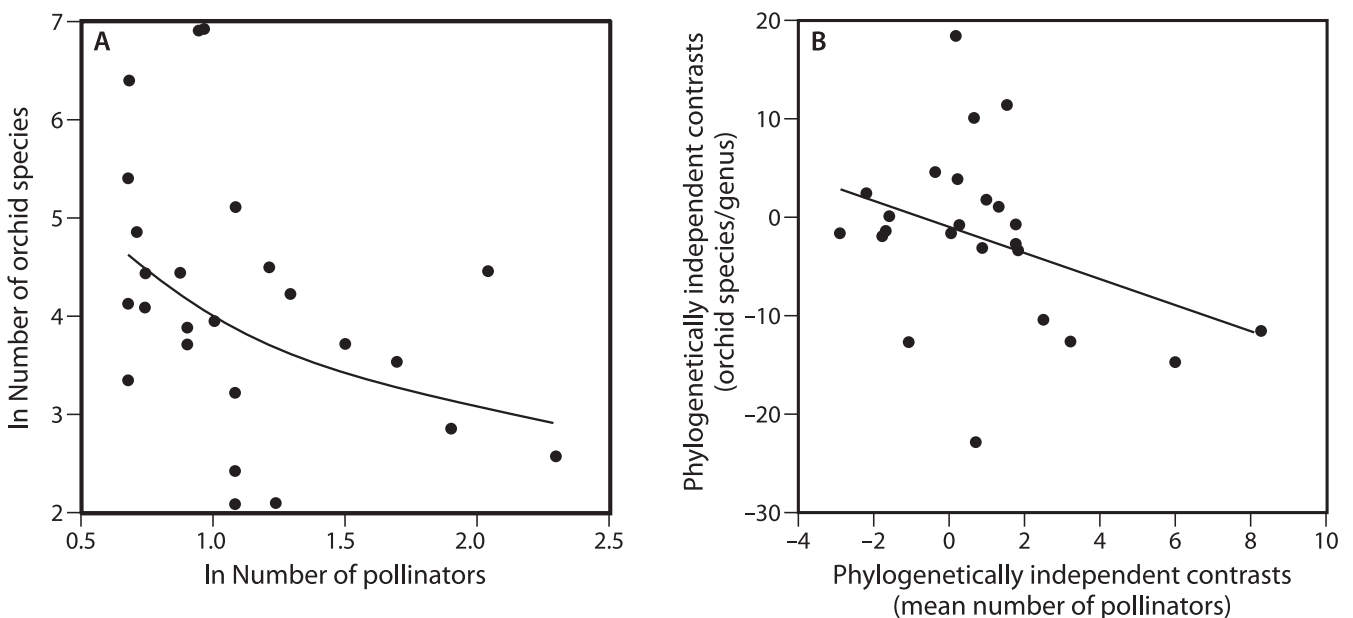

Fig. 2. Number of orchid species per genus is inversely related to the average number of pollinator species visiting each species across 27 orchid genera, based on phylogenetically unstructured **(A)** or structured **(B)** analyses. That is, orchids with a narrower range of floral visitors showed a significant tendency to speciate more per genus. Redrawn from Schiestl & Schlüter (2009).

suggest that divergence in habitat and geographical distribution often come first. This pattern mirrors the findings of Richman & Price (1992) from a phylogenetic analysis of *Phylloscopus* warblers, and earlier predictions and qualitative analysis by Diamond (1986) for New Guinean birds. The general tendency toward phylogenetic niche conservatism—that is, for daughter taxa to be ecologically similar to their ancestors—suggests that *no* adaptive shift combined with a geographic shift may often be the null expectation (Cavender-Bares & al., 2004). Crisp & al. (2009) found, in a survey of 11,000 plant species from the Southern Hemisphere, that ecological stasis at the biome level outnumbered shifts between biomes by a ratio of 25:1.

Adaptive radiation and speciation

Schluter (2000) includes rapid speciation as part of his definition of adaptive radiation, arguing that this follows usage by Simpson (1953) and that "the process characterizes all the best-known cases." However, Simpson himself stated that adaptive radiation could proceed gradually, and Schluter's second "argument" is simply reification. Givnish (1997) argued that, logically, it might be better to segregate rapid and/or extensive speciation as a testable prediction of the theory of adaptive radiation rather than part of its definition, which would preclude such tests. While speciation is an inevitable part of adaptive radiation under anyone's definition (see reviews by Givnish, 1997 and Schluter, 2000), it simply is not true that it is always accompanied by rapid or extensive speciation. In angiosperms, *Brocchinia* (Bromeliaceae)—endemic to the Guayana Shield of northern South America, and almost restricted to the extremely poor Roraima sandstone of the flat-topped tepuis and derived sands near them—has undergone an adaptive radiation in mechanisms of nutrient capture that is unparalleled at the generic level, including cases of carnivory, ant-fed myrmecophily, nitrogen fixation, and tank epiphytism, as well as the more usual uptake of nutrients from the soil (Givnish & al., 1997). Yet *Brocchinia* is a relatively small genus of ca. 20 species. It would not qualify as an adaptive radiation based on its species richness relative to its sister group, according to Guyer & Slowinski (1993), given that it is sister to the remainder of Bromeliaceae, a family of ca. 3000 species (Givnish & al., 2007). Furthermore, the present-day species of *Brocchinia* apparently diversified over the past 17 Ma—roughly the same time over which all other extant lineages of bromeliads diverged from each other. *Brocchinia* could thus hardly be said to have undergone rapid or explosive speciation, even though it manifestly has undergone a massive adaptive radiation, as indicated by its ecological diversity relative to other angiosperm genera. Moreover, *Brocchinia* has undergone much less speciation than *Navia* (ca. 80 spp.), another bromeliad genus endemic to the Guayana Shield. *Navia*, however, appears to have undergone little adaptive radiation, with most species having a very similar habit as non-impounding rosettes on sandstone outcrops. Its high species richness is almost surely due to rampant allopatric speciation based on its unique loss of long-distance dispersal due the absence of wings or other appendages on its seeds; most species are allopatric and restricted to individual tepuis. *Navia*, in other

words, appears to be analogous to fossorial rodents, rapidly speciating as a result of limited dispersibility, with little or no initial adaptive divergence (Givnish, 1997). Its rapid burst of speciation over the past 7 Ma (Givnish & al., 2007) reflects low dispersibility, not adaptive divergence. Rapid and/or extensive speciation should thus *not* be used to define adaptive radiation. Furthermore, given that judging the amount of speciation or ecological diversification within a lineage by comparisons with its sister clade (Guyer & Slowinski, 1993; Sanderson, 1998) can easily be reversed depending, for example, on the persistence or extinction of a single species sister to that lineage, it might be more appropriate to base such judgments on comparisons that include all closely related clades of comparable age, not just the sister clade.

Is adaptive radiation nevertheless associated with greater numbers of species? Yes—and no. Schluter (2000) found that island radiations of various animal and plant clades (mainly on Hawaii and the Galápagos) had a greater number of species than mainland sister groups in nine of twelve cases ($P = 0.073$ for 1-tailed binomial test); this pattern is significant ($P = 0.029$) if cases involving sister groups on other islands are also included. However, the selection of "radiations" by Schluter was seemingly arbitrary; a more appropriate set of comparisons would include *all* the radiations on a given island. The native angiosperm flora of the eight main Hawaiian Islands consists of 1004 species in 263 presumed lineages (Sakai & al., 1995; Wagner & al., 1990, 2005a). Of the 172 single-species clades, 88 consist of indigenous non-endemic species with ranges outside, leaving 175 lineages that have evolved on Hawaii (Price & Wagner, 2004). Based on the data presented by Sakai & al. (1995), Price & Wagner (2004), Givnish & al. (2009), and Harbaugh & al. (2009), the 20 most diverse lineages account for 50.7% of the native flora, and 60.7% of the flora derived in situ. That is, 7.6% of the initial colonists account for 60.7% of the autochthonous species, implying that these lineages had overall levels of species richness nearly seven times the average for the autochthonous flora, with an average of 25.5 ± 26.9 per lineage. Almost all of these lineages are clearly examples of adaptive radiation, involving a variety of traits and including such clades as the **Hawaiian lobeliads** (128 spp.—habit, habitat, mode of seed dispersal, floral form [Givnish & al., 1995, 2009]), **Hawaiian mints** (57 spp.—floral form [Lindqvist & Albert, 2002; Lindqvist & al., 2003]), ***Schiedea*** (30 spp.—habit, habitat, floral form, breeding system [Nepokroeff & al., 2005]), **Hawaiian silversword alliance** (28 spp.—habit, habitat, inflorescence form [Baldwin & Robichaux, 1995; Baldwin & Sanderson, 1998), **Hawaiian *Hedyotis*** (20 species—habit, habitat [Motley & al., 1998]), **Hawaiian *Bidens*** (19 spp.—habit, habitat [Ganders & al., 2000]), **Hawaiian *Chamaesyce*** (15 spp.—habit, habitat), and **Hawaiian *Psychotria*** (11 spp.—habitat [Nepokroeff & al., 2003]). Only one clade—*Pritchardia* (19 spp.)—appears to involve mainly geographic speciation with little ecological divergence.

Thus, at least the *largest* groups associated with adaptive radiation in the Hawaiian flora have a greater number of species than expected; indeed, the Hawaiian lobeliads appear to be the largest clade of angiosperms to have evolved on any single

oceanic island or archipelago (Givnish & al., 2009). Similar patterns occur in other large radiations in other archipelagoes, such as Macaronesia, where such examples include the *Aeonium* alliance (61 spp.—habit, habitat), the *Sonchus* alliance (31 spp.—habit, habitat), *Echium* (27 spp.—habit, habitat), *Sideritis* (27 spp.—habitat), and *Crambe* (11 spp.—habitat), all based on colonization within the last 3.3 to 15.2 Ma (Kim & al., 2008). Most of the plant radiations on Hawaii appear to have occurred over the past 5 Ma, due to the relatively small number and low maximum elevation of islands in the Hawaiian chain for several million years prior to the emergence of Kaua'i (Price & Clague, 2002; Price & Wagner, 2004). The largest radiation, that of the Hawaiian lobeliads, is an exception, having originated roughly 13 Ma ago on or near Gardner, the largest and tallest of the Hawaiian Islands over the last 40 Ma (Givnish & al., 2009).

It must be recognized, however, that the average number of species for plant clades derived in situ in the Hawaiian Islands is only 5.2, given 916 species in 175 endemic lineages (see above). If we exclude the single-species clades, so as to focus on the 94 clades for which there is at least a chance of adaptive radiation, the average clade would have only 8.9 species, despite the fact that Hawaii includes the largest islands in the central Pacific. Several small clades (e.g., *Astelia*, *Geranium*, *Hesperomannia*, *Hibiscadelphus*, *Isodendrion*, *Kokia*, *Pipturus*, *Viola*) appear to involve adaptive radiation in habit and/or habitat, have fewer than the average number of species for clades with two or more species, and have fewer species than the most closely related mainland genera where those are known. Consequently, as exemplified by the Hawaiian flora, adaptive radiation does not *necessarily* lead to extensive speciation—and indeed may be associated with lower than average number of species in many cases—although such diversification *is* involved in 19 of the largest 20 native lineages.

Can the extent of adaptive radiation be predicted?

What causes some lineages in a given region to radiate and speciate extensively and other hardly at all remains a puzzle. The usual explanations for extensive radiations are (1) early arrival of the founders, providing more time for speciation and pre-emption of ecological niches from later-arriving lineages (P.R. Grant, 1986; Carine & al., 2004; Silvertown, 2004; Linder, 2008); (2) exceptionally high amounts of heritiable genetic variation for ecologically significant traits (e.g., beak size and shape) in the founders (P.R. Grant, 1986); (3) the existence of "genetic lines of least resistance" based on the pattern of genetic covariance among several key traits (Schluter, 1996b); (4) long-standing absence of potential competitors (Simpson, 1953; Clarke & Johnston, 1996); and (5) possession of a "key innovation" that provides access to habitats or resources unavailable to other lineages (Simpson, 1953). None of these arguments can explain all cases, and a few are logically problematic. I review these issues briefly and then propose that three key, overlooked factors—*island area*, *organismal abundance*, and *interaction between limited dispersal and adaptive radiation*—whose importance should be instead be emphasized.

Early arrival. — The large radiations of Darwin's finches in the Galápagos and the honeycreepers in Hawaii originated at about the same time as the much smaller clades of Galápagos mockingbirds and Hawaiian thrushes (see P.R. Grant, 1999, Petren & al., 2005, Arbogast & al., 2006 for Galápagos; Fleischer & McIntosh, 2001, Lovette & al., 2002 for Hawaii). Lobeliads were the first large plant radiation to colonize Hawaii, ca. 13 Ma ago, and today are the largest. However, most of lobeliad diversity resides in *Cyanea*; most *Cyanea* species are endemic to single islands, with most of the variance in total species number per island related to island height and area and not to island age, except for the youngest island of Hawai'i (Givnish & al., 2009). Unless *Cyanea* has managed to invade each successive island earlier than any other lineage over the past 5 Ma, its ability to diversify at a high rate on each island has nothing to do with the initial early arrival of lobeliads. Across the nine Hawaiian plant clades whose origin has been reliably dated, there is a significant increase in ln species number (S) with age t (Fig. 3A: $r = 0.79$, $P < 0.02$; Price & Wagner, 2004). However, I note that the significance of this result is heavily dependent on inclusion of the Hawaiian lobeliads, the oldest and largest clade; if they are excluded, there is no significant relationship of ln species number to age in the remaining lineages ($r = 0.56$, $P > 0.14$). Furthermore, older clades have *lower* apparent rates of species diversification (Fig. 3B), contrary to expectations and consistent with the unbiased regression of ln S on t having an intercept >1 (Fig. 3A). Early arrival, in other words, does not guarantee higher rates of diversification in adaptive radiations.

Extensive genetic variation. — While the extraordinary morphological divergence in many adaptive radiations suggests that genetic divergence between species might be substantial, in most cases of insular radiations the reverse is true (e.g., see Baldwin & al., 1991; Givnish & al., 1995; Böhle & al., 1996; Francisco-Ortega & al., 1996). Presumably this present-day poverty of genetic variation among species reflects the recent origin of such radiations, repeated genetic bottlenecks associated with founder events, and the large effect of a few genes determining ecological and reproductive isolation (Givnish, 1997). Given that long-distance dispersal is involved with almost all founder events on oceanic islands, it is hard to imagine a plausible scenario in which some ancestral taxa could bring substantial intraspecific genetic variation to a distant island or archipelago and maintain it in the face of subsequent bottlenecks. Yet, can it be a coincidence that Darwin's finches have undergone a massive radiation in beak size and shape and that *within*-species variation in their beak dimensions are often ten times greater than that in many mainland sparrow populations (P.R. Grant, 1986)?

Evolution along genetic lines of least resistance. — This theory (Schluter, 1996b, 2000) is potentially of profound importance, in that it potentially provides an alternative explanation for the direction(s) taken by adaptive radiation. It warrants additional tests, similar to that by P.R. Grant & Grant (1995), in selection gradients on a variety of traits and the genetic covariance traits were quantified, and the observe shift in offspring traits compared with the expectation based on Lande's (1979) model. However, the fact that, often, several members

of one adaptive radiation show extensive convergence with ecologically analogous members of other radiations (see above) suggests that clade-specific differences in genetic architecture have little to tell us about the direction selection will take, while ecology has great deal to say. Furthermore, as Schluter (1996b) himself observed, genetic covariance across species may be determined partly by gene flow between populations. If natural selection drives differentiation among such populations, then seemingly strong developmental constraints may prove to be a mirage, a result of the interaction of selection and migration (Givnish, 1997). Recently, McDonald & al. (2009) showed that the repeated evolution of the WS (wrinkly spreader) morph in in vitro adaptive radiations of *Pseudomonas fluorescens* was somewhat predictable from genetics, due to the repeated occurrence of WS mutations at a few loci. However, these authors also showed that genetics did *not* ultimately provide a key as to whether *P. fluorescens* would evolve a WS morph: that morph evolved—albeit more slowly than usual—even in strains from which they removed all loci previously known to cause it.
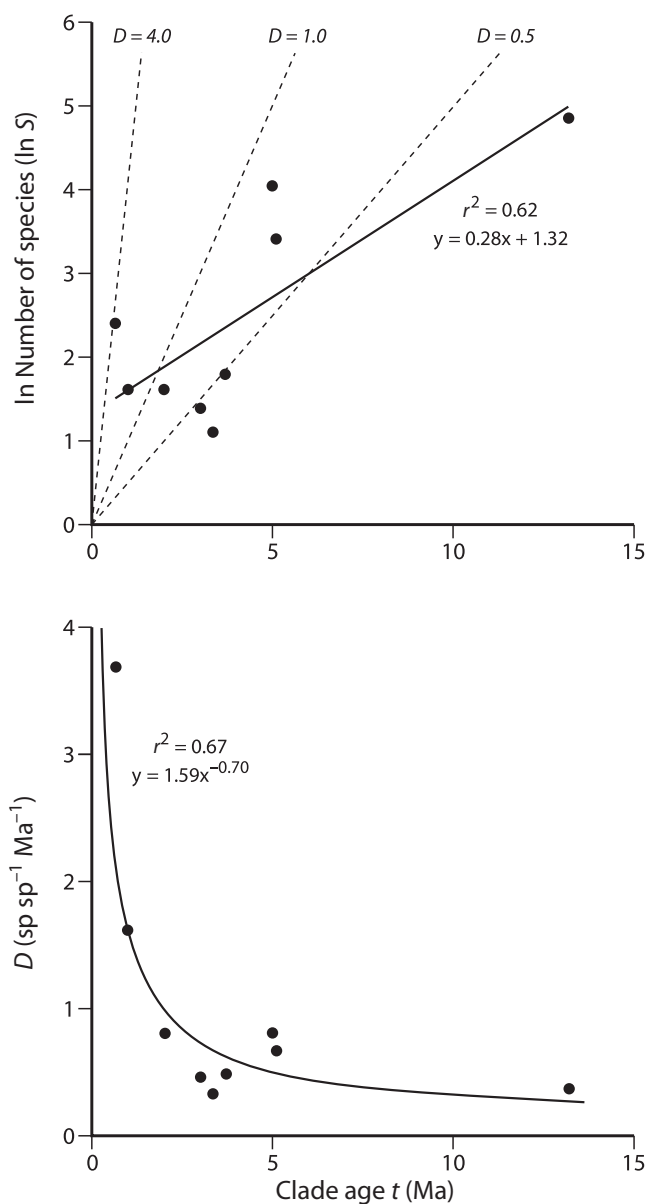
Absence of competitors. — It is logical that the absence of competitors for particular habitats or resources would foster radiation onto those habitats and resources. What is not clear is how to determine whether a specific lineage, founded by a particular ancestor, might someday compete for habitats or resources not used by that ancestor, and what kind of data on competitors, habitats, and resources present when an island or similar habitat is colonized would be needed to predict, for example, that the Hawaiian lobeliads might spawn 128 present-day species while the Hawaiian violets would generate only seven.

Key innovations. — The use of statistical tests to determine whether a particular trait is associated with greater rates of speciation, and thus is a "key innovation" (Guyer & Slowinski, 1993; Sanderson & Donoghue, 1994), is a logical means to identifying an adaptive radiation if one assumes that an increase in speciation rate is a hallmark of that process. Comparisons involving multiple clades with and without the putative key innovation provide even more powerful tests. However, such tests must also be accompanied by functional analyses or demonstrations of context-specific advantage to show that the trait(s) of concern actually increases the range of habitats or resources that can be used relative to other groups. Otherwise, traits that merely decrease dispersal ability and thereby

accelerate speciation (see above) might be confused with true "key innovations" (Givnish, 1997).

Island area. — The likelihood of speciation occurring within an island or isolated region should increase with its area, as a consequence of the greater likelihood of (1) extrinsic barriers to gene flow that could initially isolate populations from each other and promote genetic divergence (Mayr, 1942); (2) species persistence, allowing simple divergence from ancestral forms without species multiplication or lineage branching (i.e., cladogenesis), leading to anagenetic speciation and endemic species without multiplication of forms in situ (Mayr, 1970); and (3) gene flow distances being smaller than the dimensions of the island or region, allowing genetic differentiation through isolation by distance (Kisel & Barraclough, 2010). This mechanism might provide a powerful means of explaining differences in the size of adaptive radiations across islands or isolated regions, but cannot account for differences between

Fig. 3. A, number of species S vs. stem age t of nine clades in the Hawaiian flora; **B,** net rate of species diversification $D = (\ln S) / t$ as a function of stem age for the same clade. Figures are based on the data of Price & Wagner (2004) and Givnish & al. (2009). See section 5 re problems of autoregression associated with plotting D vs. t. The first panel presents a statistically unbiased analysis showing that diversification rate falls with clade age: $\ln S$ vs. t has an intercept >1, and the regression therefore cuts contours (dashed lines) of progressively lower values of D as t increases (see B). Contrary to the naïve prediction that D (sp sp^{-1} Ma^{-1} = Ma^{-1}) should increase with clade age, reflecting less ecologically saturated environments faced by early colonists, D actually declines with clade age, probably reflecting ecological saturation of individual radiations with time and their truncation as older islands subside and species restricted to them are extirpated.

radiations in the same area. Kisel & Barraclough (2010) used a meta-analysis across several broad classes of organisms to show that the minimum island area observed to support cladogenetic speciation (that is, splitting of lineages, possibly associated with adaptive radiation, unlike anagenetic speciation) increased significantly with estimates of the minimum distance required for neutral genetic differentiation among populations within species (Fig. 1). This suggests that geographic speciation

and adaptive radiation should increase with island area. Stuessy & al. (2006) examined 2640 angiosperm species in 13 oceanic and continental archipelagoes, and found that the proportion of endemic species produced by anagenetic vs. cladogenetic speciation decreased significantly with island elevation and an index for the range of habitats present, when both variables where considered separately (Fig. 4A–B). This makes sense in terms of adaptive radiation, which should increase with the range of resources available to be partitioned. Reanalysis of their data shows that the percentage of anagenetic speciation also declined significantly with island area (Fig. 4C). A multiple regression based on the data of Stuessy & al. (2006) yields highly significant drops in % anagenetic speciation with island area, elevation, and habitat heterogeneity:

$$\% \text{ anagenesis} = -0.079 \ln \text{area} - 0.207 \ln \text{elevation} - 0.253 \text{ heterogeneity} + 6.493, \qquad (1)$$

(adjusted $r^2 = 0.77$, $P < 0.001$ for 9 d.f.; $P < 0.051$ for ln area, $P < 0.040$ for ln elevation, and $P < 0.002$ for habitat heterogeneity for 1-tailed t-test). There are challenges here, especially in determining whether an initial divergence between species that later diverged anagenetically from each ancestor on a single island represents anagenesis (initial divergence between ancestors before island colonization) or cladogenesis (divergence from a common ancestor after colonization). Nevertheless, the observed pattern accords exactly with theory, in that it implies that the proportion of cladogenetic speciation, and presumably the incidence of adaptive radiation, increases with island area, elevation, and habitat heterogeneity. Island plants thus join Caribbean *Anolis* lizards, Galápagos land snails, and African rift-lake cichlids as obeying the "area rule" for adaptive radiation predicted by theoretical models (see Coyne & Price, 2000; Losos & Schluter, 2000; Gavrilets, 2004; Gavrilets & Vose, 2005; Parent & Crespi, 2006; Seehausen, 2006; Gavrilets & Losos, 2009)

Organismal abundance. — The intensity of divergent selection on sympatric populations caused by the impact of competition from one population on the other almost necessarily depends on the abundance of each competitor. If either are rare, both relative to resource supplies and to the abundance of unrelated competing taxa, then one or the other will probably have negligible selective effects on the other, and character displacement is unlikely to evolve. At least one taxon should be common, relative to resource abundance, for divergence to occur. So, although it does not appear to be part of the theoretical canon, adaptive radiation should be most likely to occur in lineages that involve that are common relative to their resources and similar competitors. Essentially, this is the flip side of
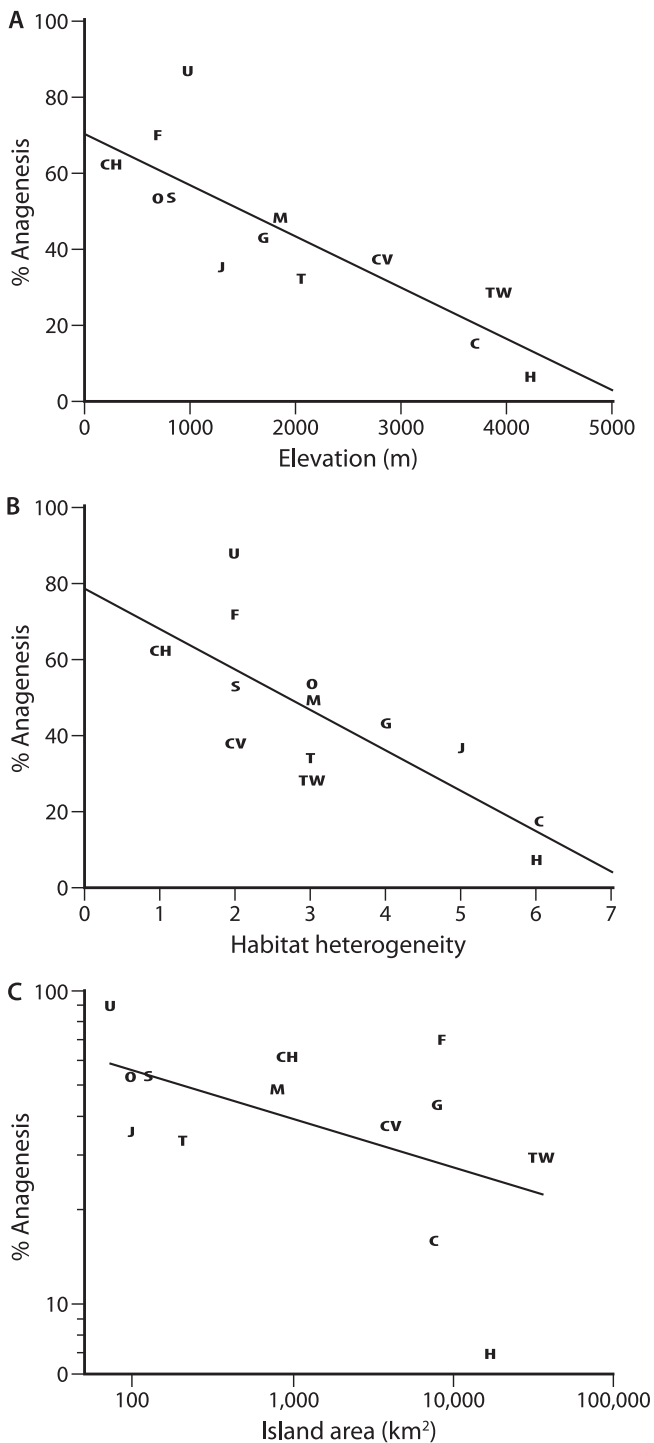
Fig. 4. Proportion of anagenetic speciation as a function of **(A)** island elevation, **(B)** range of habitats, and **(C)** island area for 13 oceanic and continental archipelagoes, based on data of Stuessy & al. (2006). Key: C, Canary Islands; Ch, Chatham Island; CV, Cape Verde; F, Falkland Islands; G, Galápagos Islands; H, Hawaiian Islands; J, Juan Fernandez; M, Madeira; O, Ogasawara; S, St. Helena; T, Taiwan; TC, Tristan de Cunha; U, Ullung.

the explanation for the relative dearth of adaptive radiation in long undisturbed mainland areas, but it should apply to both island and mainland lineages if factors other than within-clade strongly limit populations of sister taxa in sympatry.

It is interesting, in this connection, to note that the Hawaiian lobeliads—the largest radiation of plants in the Hawaiian Islands—were once the most abundant plants in the understory of rain and cloud forests there (Rock, 1919). Over the last century, however, most lobeliad species have become extremely rare and many appear to have gone extinct, apparently as a result of habitat destruction, loss of many of their honeycreeper and oʻo pollinators, and the enormous damage wrought by introduced herbivores (Givnish & al., 1995). As expected, the species that went extinct had the narrowest elevational and geographic ranges, and often were pollinated by birds with the longest, most highly specialized bills (Givnish & al., 1995). This highlights the fact that, often, the very factors that promote more speciation—in this case, limited seed dispersal and increased specialization on individual, long-billed pollinators—often promote extinction as well (Givnish & al., 1995). Members of the silversword alliance have remained abundant in many habitats (e.g., dry lava flows and open woodlands) but others have become extremely rare, apparently as a result of the depredations of introduced herbivores (Carlquist & al., 2003). Given the far-reaching effects of such exotic vertebrates, it seems unlikely that—unless we uncover more observations like those of Rock (1919) on the abundance of various plants in earlier vegetation, less disturbed by exotic vertebrates—we will make much progress relating the extent of adaptive radiation to the abundance of individual species in those radiations.

This argument might, however, provide a more satisfactory explanation for the observation by Silvertown (2004) that 20 Macaronesian genera that originated from single colonization events had, between them, given rise to 269 endemic species, while repeated colonizations by members of 20 other genera have given rise to 38 species. Silvertown (2004) and Silvertown & al. (2005) argued that earlier arriving colonists within a genus suppressed diversification due to the later arrivals, either through pre-emption of resources or hybridization. This argument seems implausible. Why should an early colonist suppress diversification from the progeny of closely related, later colonist(s) any more than it would suppress diversification by its own daughter taxa? I propose that low overall species numbers associated with multiple colonizations within a genus might instead arise through a lack of any local ecological dominance by members of that genus in the area colonized, which would be work against extensive adaptive radiation by any colonist from that genus, and would at the same permit multiple colonizations by the genus. Alternatively, if the genus in question had excellent long-distance dispersal, it would be unlikely to speciate on an island and would thus create little barrier to subsequent colonizations, which would also generate few species. A third possibility, perhaps less likely, is that multiple colonizations could maintain diverse specialist pathogens, reducing the likelihood of secondary sympatry through pathogen incompatibilities of sister populations (see Ricklefs & Bermingham, 2007; Ricklefs, 2010).

Interaction between low dispersal rate and adaptive radiation. — Limited dispersal should stimulate parallel radiations within a lineage, stimulating repeated ecological divergence and speciation in areas isolated from each other by slow migration (Givnish, 1997; Patterson & Givnish, 2004). The product should be greater amounts of speciation than would otherwise be expected, as well as convergent adaptive radiations within a clade in different regions. A prime example is the repeated radiation of African rift-lake cichlids, not only among lakes but also within lakes, with the latter reflecting philopatry to rocky shores and mouthbreeding, with these traits almost surely a result of intense predation caused by the cichlids themselves, reflecting the exceptional clear water of these deep lakes. Sexual selection for divergence in color and display behavior apparently also accelerates this process, with more species found in the deeper lakes with clearer water, and with increased rates of mismating in murkier water with dimmer light (Seehausen & al., 1997; Terai & al., 2006; Maan & al., 2010). Sexual selection in brightly lit, unusually transparent waters thus results in exceptionally brightly colored fish for freshwater habitats; presumably, a similar chain of processes (low nutrient availability → transparent water → intense predation, territoriality tied to defense of hiding places on rock outcrops or reefs → sexual selection based on visual displays → exceptionally diverse and bright coloration) underlies the bright coloration of coral reef fish as well. Repeated adaptive radiation into benthic and limnetic forms is also seen in numerous populations of three-spined sticklebacks and lake whitefish isolated in post-glacial lakes in northern North America (Schluter & MacPhail, 1993; Schluter & Nagel, 1995). Repeated evolution of up to six ecomorphs in *Anolis* lizards occupying different islands of the Greater Antilles (Losos & al., 1998) is another classic case of parallel adaptive radiations induced by restricted dispersal.

In plants, parallel adaptive radiations based on poor dispersal can be seen in *Calochortus* (Patterson & Givnish, 2004), in which serpentine tolerance has evolved seven times independently, across three mountainous regions in California and Oregon (Coast Ranges, Sierra Nevada, Cascades), and in three of the four floral syndromes associated with this genus—fairy lanterns, cat's ears, and star tulips—have also evolved several times in these same areas as well as the Great Basin and Central Mexico (Fig. 5). The evolution of a variety of base chromosome numbers has also apparently permitted *Calochortus* to "double up" its adaptive radiation by reproductively isolating three pairs of lineages and allowing them to radiate independently despite having strongly overlapping ranges (Patterson & Givnish, 2004). These pairs include the Bay Area ($x = 10$) and Coast Ranges/Sierra Nevada ($x = 7$) clades, the Pacific Northwest ($x = 10$) and Great Basin/Rocky Mountain ($x = 7$, 8, 9) clades, and the San Diego ($x = 9$) and Southwestern California ($x = 7$) clades (Fig. 5). Species within individual clades are almost always allopatric or parapatric, but species from different clades with different chromosome numbers often are sympatric, at least in part.

Cyanea, the largest genus of Hawaiian lobeliads, also exhibits parallel adaptive radiations, based on the repeated
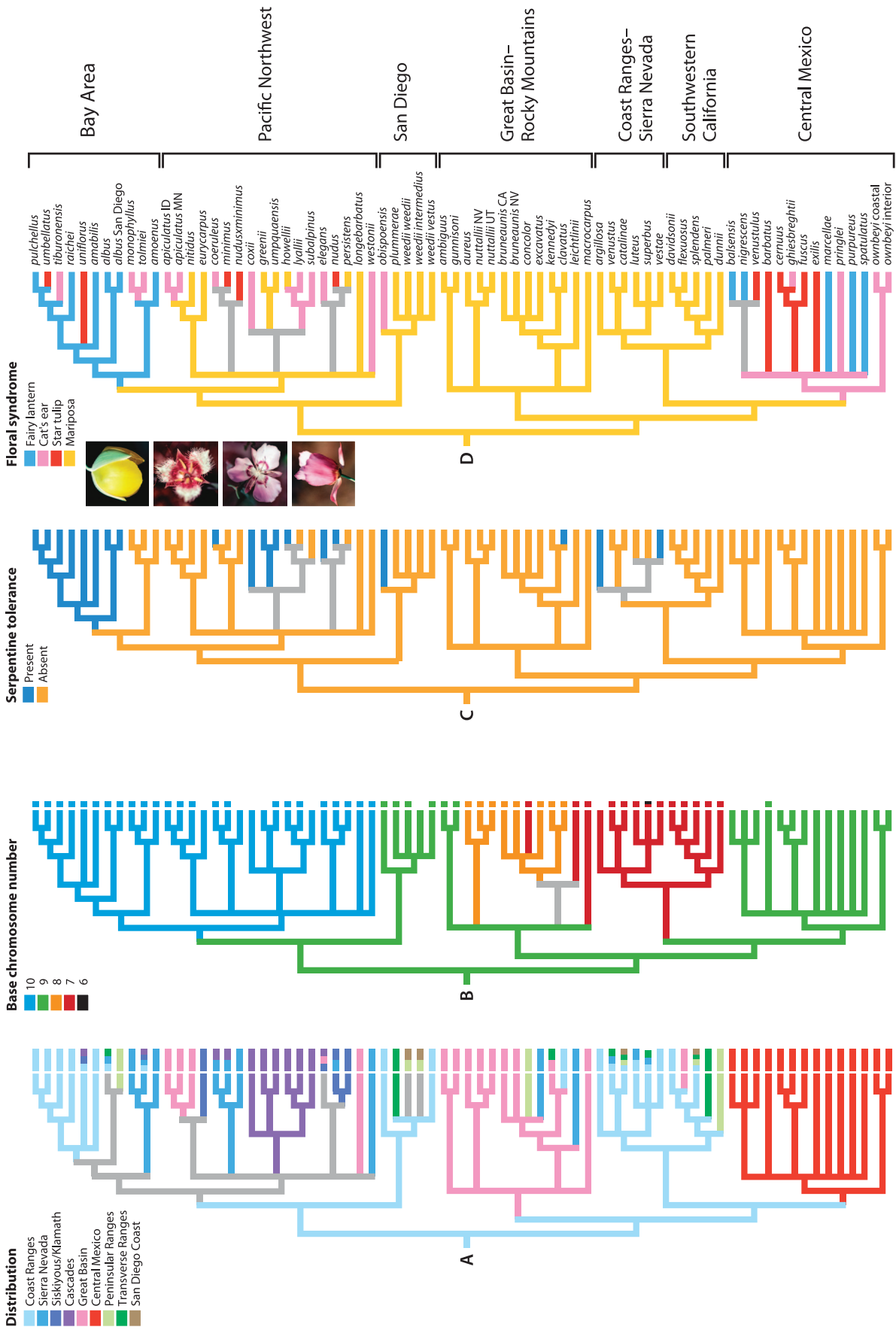
Fig. 5. Evolution of **(A)** geographic distribution, **(B)** serpentine tolerance, **(C)** base chromosome number, and **(D)** floral syndrome in *Calochortus*, inferred using parsimony. Data boxes for A and B show polymorphisms and/or missing data; hollow branches indicate equivocal resolution of ancestral state. After Patterson & Givnish (2004).

evolution of similar ranges in elevation and flower tube length on each of the four largest islands (Givnish & al., 1995, 2009). In addition, assemblages of *Cyanea* on the eight major islands show the same, tight relationship between species number and island area, with the exception of the youngest island, Hawai'i, suggesting that the saturation of adaptive radiation in *Cyanea* takes more than 0.6 Ma (the age of Hawai'i) and less than 1.5 Ma (the age of Maui, the next youngest island in the chain (Givnish & al., 2009). Interestingly, many of the species of *Cyanea* on Hawai'i are *not* restricted to that island, unlike the great majority of species in the genus, which are endemic to single islands. This again suggests that 0.6 Ma is not enough time for genetic differentiation, speciation, and adaptive radiation to run their course in *Cyanea*, but that 1.5 Ma is (Fig. 6). Inferring the time of saturation might, in some instances, be subject to reconstruction artifacts, but because Givnish & al. (2009) obtained nearly the same timeline for speciation in the Hawaiian lobeliads using both top-down and bottom-up calibrations, and because 93% of *Cyanea* species (and presumably, their ancestors) are restricted to individual islands of known geological age, support for the chronology of diversification in the Hawaiian lobeliads is excellent.

Most likely, there are many instances of massive, parallel radiations driven by adaptation to fire, poor soils, and avian polliantors, acting in concert with restricted dispersal among plants (e.g., *Banksia-Dryandra* in Australia [Mast & Givnish, 2002; Mast & al., 2005] and Proteaceae more broadly [Sauquet & al., 2009]). In the near future, we should see coordinated studies of the scale of genetic differentiation in species and of the tempo, spatial extent, and degrees of ecological divergence and endemism in such groups. The rise of specialized parasites and pathogens may also generate additional diversity within host lineages undergoing adaptive radiation, by selecting for new host taxa immune to those pathogens and thus capable of invading enemy-free space (Givnish, 1999; Agrawal & al., 2009a,b; cf. Ricklefs, 2010).
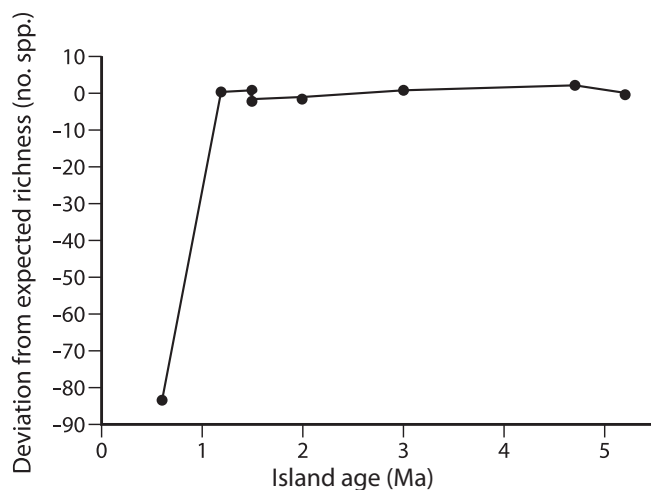
Saturation of adaptive radiation

Data on the time required to saturate adaptive radiation is currently extremely scanty for plants. As noted above, Givnish & al. (2009) estimated the time for species richness of *Cyanea* to saturate on individual islands to be greater than 0.6 Ma and less than 1.5 Ma (see Fig. 6). At a broader hierarchical scale, radiation into genus-specific habitats in the Hawaiian lobeliads occurred within 3.4 Ma after their arrival (Givnish & al., 2009). These times compare with estimates of 4 Ma required to saturate the richness of fossil equids in North America (Macfadden & Hulbert, 1988). While absolute species richness of *Cyanea* peaks on Maui and drops off sharply on Hawai'i, Givnish & al. (2009) proposed that this does not reflect any time lag between speciation and extinction—as proposed by Gillespie (2004) for *Tetragnatha* spiders and by Kassen & al. (2004) and Gavrilets & Vose (2005) for organisms generally—but was instead a result of Maui being larger and having a greater range of elevational habitats than any current island except Hawai'i, in which speciation and adaptive radiation had not run its course. The Hawaiian lobeliads thus undercut the claim and multiple explanations for supposed overshoot in adaptive radiations. The fundamental issue in cases that might involve "overshoot" is whether there can be a long lag between the competitive interactions that lead to adaptive radiation and speciation in the first place, and the contact with other competitors that is supposed to generate a drop in diversity.

On a much broader scale, Givnish & al. (2005) found that the world-wide radiation of monocot lineages into shaded habitats—marked by the independent evolution of net venation and fleshy fruits more than 20 times—appears to have taken 39 Ma to reach half-saturation, as measured by the exponential rate of decline in net lineage diversification through time. No doubt this much greater time frame reflects the limited distribution of individual lineages, and the fact that physiological and morphological adaptations to shade had to arise independently in many different continental and subcontinental areas. Both the Hawaiian lobeliads and the monocots show evidence of an initial burst of speciation and ecological diversification early in the history of a lineage, as expected on theoretical grounds (see Gavrilets, 2004; Gavrilets & Losos, 2009). Apparent variation through time in rates of net species diversification in Proteaceae restricted to the Cape floristic province—as measured by the ratio of ln species number to stem age (see figure 2C in Sauquet & al., 2009)—is low, and thus does not support the "early burst of diversification" theory, nor does the pattern of speciation and adaptive diversification seen in Bromeliaceae (Givnish & al., in prep.). Worldwide saturation of species number in *Asclepias* appears not to have occurred yet, but the genus exhibits an early burst of diversification in species number, probably starting in the Miocene, and more recently in the evolution of two of seven traits related to anti-herbivore defenses (Agrawal & al., 2009a–b). Among animals, the careful analysis of diversification rates in *Dendroica* warblers by Rabosky & Lovette (2008) did support an intial burst of speciation, while a similar analysis of whales and dolphins (Steeman & al., 2009) did not, and instead showed that rates of cetacean

Fig. 6. Saturation of species richness in *Cyanea* vs. island age, based on data and analyses of Givnish & al. (2009). Saturation requires more than 0.6 Ma (the age of the youngest island, Hawai'i) but less than 1.2 Ma (the age of Kaho'olawe) or 1.5 Ma (the age of Maui and Lana'i).

diversification peaked at times when the geographic organization of the world's oceans was being substantially modified. Much more research on the tempo and possible saturation of adaptive radiation in both plant and animal groups is needed.

■ 3. ECOLOGICAL SPECIATION IN PLANTS

Hatfield & Schluter (1999) used the term "ecological speciation" to describe cases in which selection for ecological divergence results in the evolution of traits that lead, more or less directly, to reproductive isolation. In this way, ecologically based selection for adaptive radiation can simultaneously cause the rise of mating barriers and the origin of species. The process differs from the traditional view of essentially random genetic differences accumulating between populations in allopatry, leading to partial or complete reproductive isolation when they come into secondary contact, as a result of genic or genomic incompatibilities (Dobzhansky, 1937, 1951; Mayr, 1942, 1963, 1970; Stebbins, 1950, 1971; V. Grant, 1963, 1981). Instead, different traits that are ecologically valuable in different environments (e.g., deep bodies in benthic sticklebacks, narrow bodies in limnetic forms) may themselves become the object of sexual selection and lead to the formation and perfection of interspecific mating barriers (see also Schluter, 1996a; Rundle & Schluter, 1998; Thorpe & Stenson, 2003; Rundle & Nosil, 2005; Thorpe & al., 2010).

In plants, variation in flower form and pollination biology has a unique dual role. Differences between populations in, for example, flower tube length can lead directly *both* to ecological isolation (via resource partitioning of pollinators with different kinds and sizes of mouthparts) and to reproductive isolation (via the use of different vectors to reproduce) (Givnish & al., 1995; Givnish, 1997). Speciation via shifts in pollinators may thus often involve ecological speciation (Waser & Campbell, 2004).

Schemske & Bradshaw (1999) demonstrated how plant selection by pollinating hummingbirds and bees from a F_2 hybrid swarm derived from bee-pollinated *Mimulus lewisii* and its sister species, hummingbird-pollinated *M. cardinalis*, could rapidly create strong divergent selection pressures for large "bee" flowers low in anthocyanin and carotenoid pigments, and for "hummingbird" flowers rich in nectar and anthocyanins. One allele that increased petal carotenoid concentration decreased bee visitation by 80%, while another that increased nectar production doubled hummingbird visitation. Subsequently, Bradshaw & Schemske (2003) found that near-isogenic lines (NILS) of *M. cardinalis* with insertion of the *M. lewisii*-derived *YUP* allele (producing yellow petal carotenoids) produced dark pink flowers that were visited 74 times more frequently by bees than the wild type, while *M. lewisii* NILS with insertion of the *M. cardinalis*-derived *yup* allele (coding for an absence of yellow carotenoids) produced yellow-orange flowers that were visited 68 times more frequently by hummingbirds. This suggests that substitution of one allele for another at a single locus could provide a large measure of reproductive isolation via a pollinator shift. Despite the virtual absence of any post-mating barrier to crossing between *M. lewisii* and *M. cardinalis*, field studies found nearly complete pollinator-mediated reproductive isolation, with only 0.1% of seeds collected in the wild yielding F_1 hybrids (Ramsey & al., 2003).

These findings results suggest that pollinator shifts could lead to speciation in *Mimulus* or other plant genera (e.g., see Dressler, 1968) even in sympatry. However, as noted by Coyne & Orr (2004), this would require the co-occurrence of a new mutation, a new pollinator preadapted to that mutation, and pollinators sufficiently faithful to result in complete reproductive isolation almost immediately. The "mutants" studied by Bradshaw & Schemske (2003) had lower fitness than the parental forms, and could not replace them unless there were a major shift in the abundance of pollinators; I would argue, however, that reduced fitness in this case may simply be a product of the inbreeding used to establish near-isogenic lines, and may not be a general impediment to speciation. More importantly, however, initial degrees of divergence are likely to produce "leaky" mating bariers (e.g., see Dilley & al., 2000; C.D. Smith & al., 2008). Continued gene flow between populations could thus prevent initial floral divergence and a shift toward a new pollinator. After such a shift occurred in allopatry, however, selection for reinforcement could proceed rapidly. Continued allopatry would, of course, greatly strengthen reproductive and ecological isolation (see Fulton & Hodges, 1999; Ramsey & al., 2003; Coyne & Orr, 2004). Very strong pollinator preferences, however, can drive ethological isolation of plant species based on their pollinators even in sympatry (Gegear & al., 2007). Dilley & al. (2000) found that many co-occurring species of *Calochortus* differed quantitatively in their visitation by different pollinators, but that the observed overlap in such visitors would be inadequate to result in reproductive isolation. Patterson & Givnish (2004) thus argued that the observed diversification in floral syndromes within subclades of *Calochortus* should be seen as a "consequent radiation", with selection for local divergence in habitat driving the secondary adaptation of flowers to the range of pollinators and abiotic conditions found in different habitats. Fairy lanterns restrict access to highly faithful bee pollinators, and may be analogous to long-tubed, exclusionary forms seen in hummingbird-pollinated flowers under closed canopies in Neotropical forests. Hairs on the inner surfaces of cat's-ear flowers may trap heat in their cool, high-elevation habitats. Mariposas and star tulips produce large, brightly colored flowers adapted to open sites that are brightly illuminated with broad-spectrum light (Givnish & Patterson, 2000). Mariposas, which grow in drier environments, hold their petals nearly erect, which may reduce evaporation for a given petal area. In general, we should look for relatively low "leakage" of pollinator visits between sister plant species involving a pollinator shift in at least one as a sine qua non for ecological speciation. Cases of such shifts in sympatry or peripatry would make for a more airtight conclusion.

Sexual selection may often be the primary force driving ecological speciation via pollinator shifts in plants. Hodges & Arnold (1995) and Hodges (1997) proposed that such selection, mediated by floral visitors, may underlie the rapid radiation of the columbines (*Aquilegia*) and other plant lineages with spurs. Different spur colors, shapes, lengths, or orientation can attract
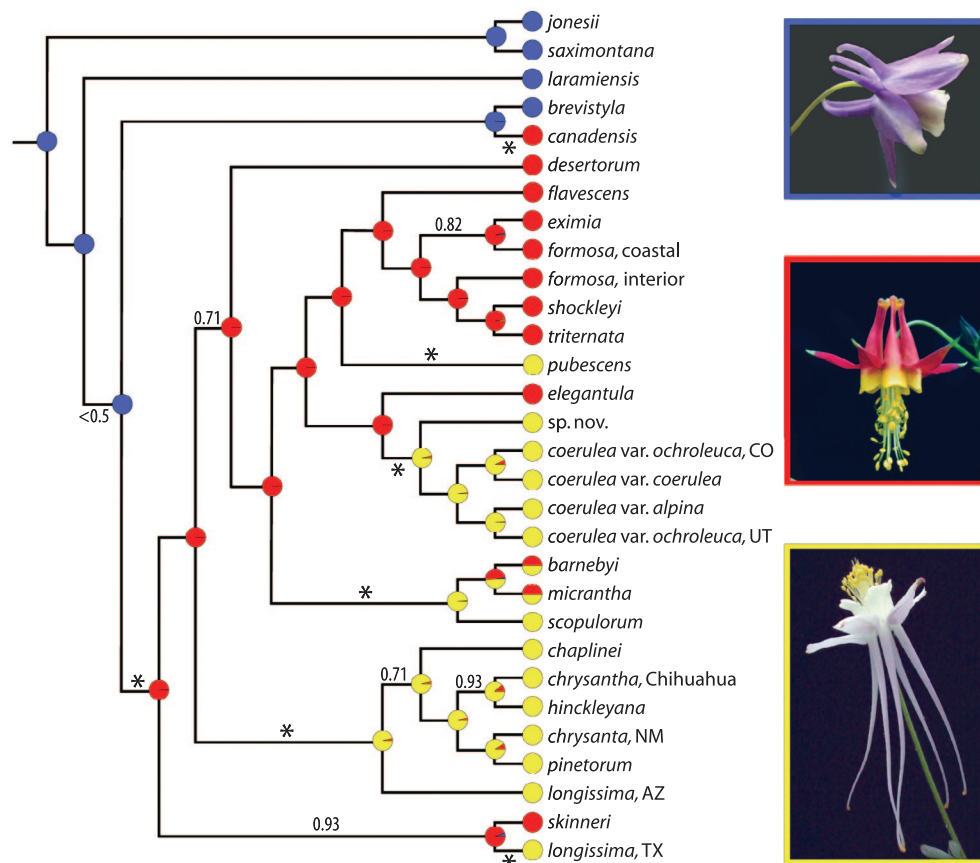
different pollinators to quite different degrees. Experimentally shifting the posture of the flowers of *A. pubescens* from upright to pendent (like those of hummingbird-pollinated *A. formosa*) reduced hawkmoth visitation 10-fold. Trimming nectar spurs of *A. pubescens* did not decrease hawkmoth visitation or increase that by hummingbirds, but it did reduce the seed set effected by hawkmoths by preventing them from fully penetrating the spurs to obtain nectar and thus contacting the sexual parts of the flower with their head and proboscis (Fulton & Hodges, 1999).

In seven of eight cases, plant lineages with nectar spurs show a higher rate of net species diversification than sister clades without spurs (Hodges, 1997). On average, clades with spurs were associated with a 16-fold increase in species number relative to their unspurred sisters. Furthermore, among the 25 species of North American *Aquilegia*, pollinator shifts were always associated with an increase in spur length, with two shifts from bees to hummingbirds, and five from hummingbirds to hawkmoths (Fig. 7; Whittall & Hodges, 2007). Given that North American *Aquilegia* radiated rapidly within the last 1.4–5.0 Ma (Bastida & al., 2010), probably most or all of these shifts reflect adaptation to pre-existing pollinators, rather than ongoing coevolution between *Aquilegia* and its pollinators. Directional selection for longer spurs should result when plants shift to longer-tongued pollinators, perhaps in the absence of their preferred pollinator. Under those conditions, flowers with longer spurs should increase the chance of transferring pollen

successfully from the anthers to the pollinator (Darwin, 1862; Whittall & Hodges, 2007). It should be more difficult to evolve shorter spurs, given that it would initially decrease plant fitness by reducing pollen transfer to the pollinator. It is unclear, however, why a transition to a locally more common, short-tongued pollinator could not occur first, followed by evolution of shorter spurs. The advantages of longer spurs in promoting speciation via shifts to pollinators with longer mouthparts must be set against the disadvantage of increased risks of extinction associated with specialized adaptation to more specialized mutualists (see Givnish & al., 1995), a process not recorded in the phylogeny inferred from extant taxa (Fig. 7).

The association of higher speciation rates with nectar spurs should extend to many more plant groups that have simply undergone a shift from bowl- to gullet-shaped flowers. Once a floral tube is in place, simple changes in the timing of tube development (i.e., allochronic evolution) could change the length of that tube and rapidly adapt plants to pollinators with long or shorter mouthparts/bills (e.g., see Rodríguez-Gironés & Llandres, 2008). The exclusionary apparatus provided by the floral tube would also tend to specialize flowers for visits by only a small number of potential visitors and create incipient mating barriers. By contrast, mechanical isolation would be much more difficult in plants with open, bowl-shaped flowers. The much greater number of species of Iochrominae (Solanaceae) with long flower tubes, adapted for hummingbird and hawkmoth pollination, compared with the small number of

Fig. 7. Evolution of floral adaptation to bumblebees, hummingbirds, and hawkmoths in North American *Aquilegia*, superimposed on the majority-rule consensus Bayesian cladogram. The probability of each syndrome occurring at ancestral nodes is indicated with pie charts at each node. Inferred shifts in pollination syndromes are shown by asterisks, including two from bumblebee to hummingbird pollination, and five from hummingbird to hawkmoth pollination. All inferred shifts involve an increase in the lengths of spurs and pollinator mouthparts. After Whittall & Hodges (2007).

fly- or bee-pollinated species with short floral tubes (see figures in S.D. Smith & Baum, 2006 and S.D. Smith & al., 2008) appears to be consistent with this hypothesis.

Genera showing an unusually high proportion of pollinator shifts (ca. 20% to 47%) include *Platanthera* of the Northern Hemisphere (Hapeman & Inouye, 1997), *Costus* of the Neotropics (Kay & al., 2005), Iochrominae of South America (S.D. Smith & Baum, 2006; S.D. Smith & al., 2008), and *Aquilegia* of North America (Whittall & Hodges, 2007). *Disa* of South Africa and Polemoniaceae of tropical and temperate America are characterized by numerous pollinators and, pending modern analyses using overlays on independent molecular phylogenies, most likely also involve numerous pollinator shifts (see V. Grant & Grant, 1965; S.D. Johnson & al., 1998; S.D. Johnson, 2000, 2005; S.D. Johnson & Brown, 2004; L.A. Johnson & al., 2008). All seven of the pollinator shifts in Neotropical *Costus* involve a transition from orchid bees to hummingbirds, consistent with the pattern seen in *Aquilegia. Platanthera* involves seven classes of pollinators, plus selfing; of 17 pollinator transitions, 5 are from night-flying, noctuid and pyralid settling moths to night-flying hawkmoths (Fig. 8). I note that pollinator shifts and floral syndromes in *Platanthera* appear to be responsive to environmental conditions and pollinator sensory capabilities. The two origins of brightly colored, yellow or purple flowers occurred in open habitats with bright, wide-spectrum illumination, in which such visually conspicuous displays would be seen to best effect. Shifts to pollination by butterflies or day-flying hawkmoths also occurred in open habitats, consistent with the sensory modalities of those insects.

Context-dependent sexual selection may also be responsible for the widespread occurrence of visually inconspicuous, small flowers with whitish, creamy, or greenish petals in tropical forests, especially in dimly lit understories. As argued by Givnish & Patterson (2000), low levels of narrow-spectrum, greenish light in forest understories do not favor the evolution of large, brightly colored petals. This argument also applies to the evolution of visually inconspicuous flowers in temperate forest herbs that bloom after the tree canopy has expanded (e.g., *Aplectrum, Medeola, Osmorhiza, Polygonatum, Tipularia*), in contrast to the brightly colored, large-petaled forest herbs of early spring (e.g., *Anemone, Erythronium, Sanguinaria, Trillium, Uvularia, Viola*) or of evergreen forest understories (e.g., *Goodyera, Mitchella, Scoliopus*). Selection for small, visually inconspicuous flowers in forest understories presumably puts a premium on the use of scents as floral attractants. Selection for such flowers in tropical forest understories, based on dim, narrow-spectrum lighting, and for fleshy fruits under such windless conditions, are preconditions for the repeated evolution of dioecy (Bawa, 1980; Givnish, 1980).

Finally, there is ample evidence that reproductive isolation can evolve rapidly through shifts in flowering phenology, which could, in turn, lead to reproductive isolation. Franks & al. (2007) and Franks & Weis (2008) found that five years of drought in central California caused a shift to earlier flowering, longer duration of flowering, reduced peak flowering, and flowering at an earlier age and smaller size in the annual crop *Brassica rapa*, based on comparisons with plants grown from seed stored each year. Savolainen & al. (2006) argued that divergence in flowering time, perhaps associated with a shift in substrate, was the basis for sympatric speciation in the palms *Howea forsteriana* and *H. belmoreana* on Lord Howe Island, although it is not clear how large the island was when the species diverged (Stuessy, 2006). Today, *Howea* occurs in 70% of the natural vegetation and its two wind-pollinated species co-occur in ca. 20% of their current range, so flowering phenology appears to be the primary means of reproductive
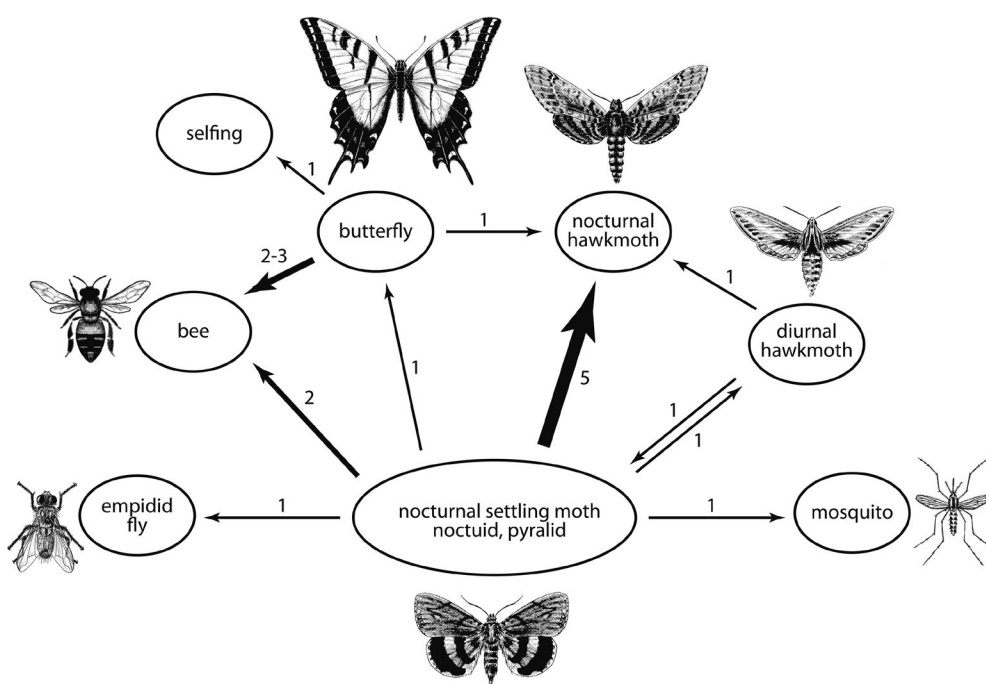

Fig. 8. Summary of 17 inferred shifts in pollinators among the 36 species of *Platanthera* from North America and East Asia studied by Hapeman & Inouye (1997). Note key role of settling moths as "source" pollinators; of nocturnal hawkmoths as "target" pollinators; and of butterflies as "unstable" intermediary pollinators. After Hapeman & Inouye (1997).

isolation. The pattern of genetic divergence between the species—concentrated in just a few loci—is more consistent with rapid sympatric divergence than prolonged allopatric divergence. Initial divergence based on substrate, followed by selection for reproductive isolation via phenology, seems unlikely to have promoted the initial divergence between populations, unless reproductive individuals today are more restricted to volcanic vs. calcarenite substrates than the populations to which they belong.

■ 4. ECOLOGICAL ASPECTS OF HOMOPLOID HYBRID SPECIATION

Early in the Modern Synthesis, the contributions of hybridization to speciation and ecological divergence were viewed primarily as negative. When populations that had diverged in isolation came back into secondary contact, in some cases reproductive isolation would not be complete. The outcome of such contact could be (1) **stable hybrid zones,** balancing selection against hybrids with constant migration of new individuals from both populations to the hybridizing front; (2) successful selection for **reinforcement** of reproductive isolating mechanisms and completion of allopatric speciation; (3) reproductive **fusion** of the partially differentiated populations, negating speciation and creating an ephemeral clinal gradient of genetic variation as gene flow overwhelms selection; and (4) **polyploid speciation,** in which fusion of unreduced gametes from one or both parents leads to polyploid progeny, which are reproductively isolated by karyotype from parental forms more or less immediately (Mayr, 1942; Stebbins, 1950).

Today, we recognize that the effects of hybridization and reticulate evolution on speciation and adaptive diversification can be far more complex (V. Grant, 1981; Rieseberg & al., 1988, 1996, 1999; McCarthy & al., 1995; Rieseberg, 1997, 2000, 2006; Ungerer & al., 1998; Barton, 2001; Wolf & al., 2001; Gross & Rieseberg, 2005; Arnold & al., 2008; P.R. Grant & Grant, 2008; P.S. Soltis & Soltis, 2009). Here I focus on two key features of homoploid (i.e., non-polyploid) hybridization that shift the trajectories of ecological evolution in important ways, involving **transgressive hybridization** and **introgression of adaptive gene combinations,** based largely on the superb work by Loren Rieseberg and his colleagues. Polyploid speciation—an unusually common phenomenon in plants and rare in animals—has already been reviewed extensively, in the recent past (e.g., P.S. Soltis & Soltis, 2000; Paun & al., 2007, 2009; Pires & Hertweck, 2008; P.S. Soltis & Soltis, 2009; D.E. Soltis & al., 2009; Wood & al., 2009) and in this symposium (D.E. Soltis & al., 2010).

Transgressive hybridization. — F_1 hybrids are often phenotypically intermediate between the parental taxa; F_2 hybrids and early backcrosses produce a much wider range of phenotypes, but the traditional view of these and of hybrid species had long been that they are also phenotypically intermediate between the parental taxa (Wiegand, 1935; Riley, 1938; Anderson, 1948, 1949; Heiser, 1949; Stebbins, 1959). If this were always so, it would be difficult for hybrids to be ecologically isolated from their parents unless those taxa were substantially

divergent ecologically from each other. Under those circumstances, F_1 hybrids might persist in "hybrid habitats" intermediate between those of the parental taxa. This scenario was first advanced for *Iris fulva* and *I. hexagona* and their apparent hybrids in Louisiana (Riley, 1938; Anderson, 1948). *Iris fulva* typically grows on shady, relatively well-drained sites, while *I. hexagona* grows on open, wetter sites. Anderson (1948) argued that human disturbance might favor such hybrids by breaking down the habitat barriers separating closely related species and allowing them to hybridize in the first place, and then by reducing competition and thus allowing some of the F_2 hybrids and backcrosses to coexist locally (see also Templeton, 1981). Using plastid and nuclear markers, Arnold & al. (1990, 1991) and Arnold (1993) demonstrated that the stabilized Louisiana hybrid species *Iris nelsonii* is a result of hybridization and introgression (i.e., gene flow into one taxon through hybridization with other species and repeated backcrosses with the first) involving *I. fulva*, *I. hexagona*, and *I. brevicaulis*. In its narrow range, *I. nelsonii* grows in a hybrid habitat (shaded but quite wet sites). Based on results from greenhouse studies and field transplants, Martin & al. (2005, 2006) showed that flooding tolerance increased with the extent of *I. fulva* markers in backcrossed *I. brevicaulis*, and that drought tolerance increased with the extent of *I. brevicaulis* markers in backcrossed *I. fulva*. These studies confirmed Anderson's (1949) claim that "A trickle of genes so slight as to be without any practical taxonomic result might still be many times more important than mutation."

Overturning the traditional view, a great deal of evidence has now accumulated to show that hybridization can frequently generate *transgressive segregation*, producing phenotypes that lie outside the range of the parental phenotypes (Rieseberg & Carney, 1998; Rieseberg & al., 1999, 2003). Such transgressive hybridization can be a powerful creative force, assembling distinctive phenotypes that may greatly extend the ecological range of habitats and associated adaptations in a lineage and thereby facilitate adaptive radiation. Rieseberg & al. (1999) surveyed 171 studies involving crosses among inbred lines, populations, and closely related species of various animals and flowering plants and found that transgressive segregation was surprisingly common: 91% of studies reported at least one transgressive trait, and 44% of 1229 traits were transgressive in at least certain cases. The mechanism appears to involve the occurrence of complementary genes in closely related lines, which shift the expression of a quantitative trait in the genetic background of one species toward the phenotype of the other, and vice versa. Such complementary action—or epistasis involving several genes—should increase with genetic distance between lines. Stelkens & Seehausen (2009) confirmed this, finding that transgression frequency increased with genetic distance in eudicots in highly significant fashion, explaining 43% of the variance in transgression frequency. For F_2 hybrids among African rift-lake cichlids, genetic distance accounted for 78% of the variance in the occurrence of transgressive phenotypes (Stelkens & al., 2009). Transgressive segregation thus appears to be more likely for crosses between more distantly related parents. Reduced viability or fecundity of the progeny

of such crosses may therefore reduce the role of transgressive hybridization somewhat, but its widespread occurrence despite this limitation suggests that transgressive segregation is an important evolutionary process not anticipated by the Modern Synthesis. Models indicate that homoploid hybrid speciation it favored by substantial reproductive barriers between the parental taxa, by partial or complete geographic isolation of the initial hybrids from them, and by novel chromosomal arrangements and habitats for the hybrid species (see Buerkle & al., 2000, 2003; Rieseberg, 2006). It should be noted that hybridization appears to be more likely to lead to speciation in plants if followed by polyploidization (Buggs & al., 2009).

Early research by Rieseberg and his colleagues (Rieseberg & al., 1988, 1990a,b, 1991a,b; Dorado & al., 1992) confirmed a substantial fraction of prior work by Charles Heiser suggesting that hybridization and introgression involving the widespread common sunflower (*Helianthus annuus*) and several of its congeners led to the formation of a new species and introgressed races. In addition, Rieseberg (1991) and Rieseberg & al. (1991a) demonstrated the unsuspected hybrid origin of *H. anomalus*, *H. deserticola*, and *H. paradoxa*, apparently from independent, repeated crosses of *H. annuus* and *H. petiolaris*. The three ancient hybrids have narrow geographic ranges but together span a greater ecological range than the rest of *Helianthus* sect. *Helianthus* combined: *H. anomalus* occurs on sand dunes in Utah and northern Arizona; *H. deserticola* grows in deserts of the Great Basin in Nevada, Utah, and northern Arizona; and *H. paradoxa* lives in saline wetlands in Texas and New Mexico (Rieseberg, 2006). One parent, *H. annuus*, inhabits heavy clay soils across much of the Great Plains, the Great Basin, the desert Southwest, Idaho, California, and semi-arid Oregon and Washington. The other parental taxon, *H. petiolaris*, occupies sandy soils over large areas of the Great Plains and Great Basin. Narrow (ca. 30 m) hybrid zones frequently form where populations of *H. annuus* and *H. petiolaris* come into contact where soils change abruptly. As expected from their divergent ecology, the three ancient hybrid species differed substantially from the parental taxa when all were grown in a common garden. In a survey of 40 morphological, life-history, and ecophysicological traits, Rieseberg & al. (2003) found that *Helianthus anomalus* differed from its parent in 20 traits (8 with intermediate expression, 12 with transgressive expression); *H. deserticola*, in 16 traits (4 intermediate, 12 transgressive); and *H. paradoxa*, in 24 (8 intermediate, 16 transgressive). Overall, this points to 60% to 75% of the divergent traits in ancient hybrids arising from transgressive expression. Comparisons based on greenhouse and in situ field studies demonstrated that 68% to 100% of the observed amounts of transgressive expression in the ancient hybrids lay within the range seen in artificial, doubled backcrossed populations derived from the two parental species (Lexer & al., 2003a; Rieseberg & al., 2003; Gross & al., 2004; Ludwig & al., 2004). The sand-dune specialist, *H. anomalus*, has several traits typical of sand-dune endemics, including heavy cylindrical seeds, rapid root growth, and succulent leaves. *Helianthus deserticola* exhibits many of the characteristics of winter annuals, including early flowering, short stature, and narrow leaves. Finally, *H. paradoxa* shares

several traits with other halophytes, including leaf succulence and reduction of mineral ion uptake (Rosenthal & al., 2002; Welch & Rieseberg, 2002; Lexer & al., 2003b, 2004; Donovan & al., 2009; Edelist & al., 2009). Its increased viability in salt marshes relative to its parents traces, at least in part, to transgressive segregation of a salt-tolerance gene (CDPK3) and two other quantitative trait loci (QTLs).

Taken as a whole, these findings argue strongly that transgressive hybridization and ecological selection have played a central role in speciation and ecological divergence in North American sunflowers. Complementary to these findings, Rieseberg and his colleagues found that (1) reductions in pollen fertility among artificial hybrids of *Helianthus annuus* and *H. petiolaris* were largely eliminated in four generations; that (2) the ancient hybrids have strong crossing barriers associated with chromosomal re-arrangements; and that (3) the ancient hybrids have genomes that, based on QTL analyses, represent somewhat similar patterns of genetic recombination of the parental genomes. Hybrid speciation facilitated by transgressive expression of ecological traits has been proposed for *Codia* (Cunoniaceae) on New Caledonia (Pillon & al., 2009) and *Senecio* (Hegarty & al., 2008; Rieseberg, 2009) among plants, and for African rift-lake cichlids (Albertson & Kocher, 2005; Stelkens & al., 2009) and Sulawesi sailfin silversides (Herder & al., 2006). Similar arguments based on transgressive expression of reproductively important traits have been advanced for *Heliconius* butterflies (Melo & al., 2009) and European lake whitefish (Renault & al., 2009; Woods & al., 2009).

Introgression of adaptive gene combinations. — Movement of ecologically adaptive genes and gene combinations from one species to another via hybridization and introgression have been rigorously demonstrated for *Helianthus* (see previous section), *Senecio* (Rieseberg, 2009), and *Iris* (Taylor & al., 2009). As proposed by Anderson (1949), even limited gene flow via introgression—undetectable or nearly so by standard taxonomic methods—can increase the range of ecological possibilities available in an important way and thus play a creative role in adaptive evolution (see also Stebbins, 1959; V. Grant, 1981). Seehausen (2004) has advanced the "hybrid swarm" hypothesis for adaptive radiations, noting that (1) recent hybridization and introgression greatly increases genetic variation at large numbers of loci; (2) greater genetic variation can lead to more rapid response to ecological selection for divergence; and (3) many young adaptive radiations appear, based on discordances near the base of nuclear and cytoplasmic DNA phylogenies, to have had a hybrid or introgressed origin—as exemplified by the Hawaiian silversword alliance (Baldwin & al., 1991; Baldwin & Sanderson, 1998; Barrier & al., 1999), Hawaiian *Laupala* crickets (K.L. Shaw, 1996, 2002), Lake Baikal sculpins (Hunt & al., 1997; Kontula & al., 2003), three radiations of cichlids from the African rift lakes (P.W. Shaw & al., 2000; Salzburger & al., 2002; Terai & al., 2002; Seehausen & al., 2003; Verheyen & al., 2003), *Heliconius* butterflies (Beltran & al., 2002; Gilbert, 2003), and Darwin's finches (Petren & al., 1999; Sato & al., 1999; P.R. Grant & Grant, 2009). This is an extremely important idea that needs further exploration. Within Darwin's finches, low but fairly consistent levels of hybridization and

introgression occur among a number of species (P.R. Grant & Grant, 2009) and are thought to have played a key role in maintaining *Geospiza fortis* on Daphne Major after the major El Niño event of 1982–83 by introducing genes from the occasional visitor *G. fuliginosa* and allowing introgressed *G. fortis* to survive on a diet of small soft seeds unlike those *G. fortis* usually consumes (P.R. Grant & Grant, 1992, 1996; B.R. Grant & Grant, 1993). The idea of a **syngameon** (Lotsy, 1925; V. Grant, 1981)—of a complex of selectively maintained, ecologically distinct but genetically close species that can occasionally exchange genetic material—lies at the heart of current thinking by Ole Seehausen & Peter and Rosemary Grant on the causes of rapid diversification, and it bridges the roles of adaptive radiation, hybridization, and subsequent selection for reproductive reinforcement. Verne Grant (1981) suggested that the diversity of such species-rich groups as North American *Aquilegia*, *Gilia*, *Iris*, *Mimulus*, *Pinus*, and *Quercus* reflected their status as syngameons. Groups that generate numerous species through cladogenetic speciation would also, of course, provide much material for additional hybridization and subsequent speciation.

Today, hybridization and introgression might facilitative the transfer of genes from crop plants to their wild relatives and make them more pernicious weeds. Twelve of the world's most important crops—including wheat, rice, corn, sorghum, and soybean—hybridize with uncultivated congeners in some part of their distribution (Ellstrand & al., 1999). There is ongoing concern that insertion of advantageous traits into crops via genetic engineering could "leak" into weedy wild relatives and wreak havoc in cultivated or natural ecosystems (Stewart & al., 2003). Another concern is the possible extinction via genetic swamping of rare species based on introgression or hybridization involving more abundant relatives (Levin & al., 1996). Examples include the swamping or assimilation of *Cercocarpus traskiae* on Santa Catalina Island by *C. betuloides* (Rieseberg & Gerber, 1995), *Argyranthemum coronopifolium* by *A. frutescens* in the Canary Islands (Levin & al., 1996), and *Gossypium tomentosum* by the introduced *G. barbadense* in Hawaii (DeJoode & Wendel, 1992).

■ 5. ECOLOGICAL DETERMINANTS OF NET DIVERSIFICATION RATES AND OVERALL SPECIES RICHNESS

If genetic variation and hybridization/introgression provide the raw material for speciation, and if adaptive radiation and ecological speciation supply the impetus for divergence, ecological isolation and, ultimately, reproductive isolation, then what limits the number of species that can arise in a region, the rate at which they arise, and the ecological range they collectively span? This question is very complex, and one that ecologists and evolutionary biologists have mulled since G. Evelyn Hutchinson (1959) published his famous essay, "Homage to Santa Rosalia, or why are there some many species of animals." It is a question seemingly removed from the issue of immediate concern—plant speciation—but limits on regional plant species richness and net rates of plant diversification place fundamental constraints

on the degree to which selection for genetic divergence within species, adaptive radiation, and ecological speciation, operating across lineages, and possibly varying through time and limited by diversity-dependent feedbacks, can produce plant species richness and functional diversity, and vice versa.

Rates of net diversification. — The effect of a particular trait or environmental feature on the rate of net species diversification (i.e., the difference between the rates of speciation and extinction) can be analyzed by (a) comparing the numbers of present-day species in several pairs of sister clades with and without that trait or feature (e.g., Farrell & al., 1991; Dodd & al., 1999; Heilbuth, 2000; Barraclough & Savolainen, 2001); (b) making the same comparison between sets of clades with and without the trait/feature, irrespective of their relationships to each other (e.g., Eriksson & Bremer, 1992; Ricklefs & Renner, 1994, 2000); (c) calculating the net rate of diversification, based on pure-birth or mixed birth-death models and using estimated crown- or stem-group age and the number of present-day species for several clades with and without the trait/feature (e.g., Stanley, 1979; Eriksson & Bremer, 1992; Magallón & Castillo, 2009); and (d) fitting pure-birth and mixed birth-death models for speciation and extinction to the number of species inferred to be present within a lineage at different times in the presence/absence of the trait or feature (e.g., Rabosky & Lovette, 2008; Agrawal & al., 2009a,b; Steeman & al., 2009). New approaches also include Bayesian analysis of waiting times in single phylogenies (Ree, 2005), likelihood ratio tests (Paradis, 2005), and phylogenetically corrected correlation (Freckleton & al., 2008).

Based on approaches (a)–(d), several recent studies have shown that net rates of diversification are significantly higher in:

(1) *Herbs vs. woody plants* (Eriksson & Bremer, 1992; Ricklefs & Renner, 1994, 2000; Dodd & al., 1999). – Herbaceous lineages have roughly four times as many species as their sister lineages, and herbaceous families overall have roughly three times as many species as woody families. This striking pattern, based on comparisons among hundreds of families of flowering plants, most likely reflects the shorter generation time of herbs and their general tendency to diverge genetically from each other more rapidly than slower-growing, longer-lived woody plants (Gaut & al., 1992; Givnish & al., 1999; S.A. Smith & Donoghue, 2008), as well as the ability of smaller plants to partition environmental heterogeneity in more fine-grained fashion (Ricklefs & Renner, 1994). In addition, most herbaceous families have small seeds unspecialized for long-distance transport (Ricklefs & Renner, 1994); such plants tend to show genetic differentiation within species at the smallest spatial scales (Vekemans & Hardy, 2004; Hardy & al., 2006). Most herb families are also animal-pollinated (Ricklefs & Renner, 1994), and zoophily is strongly associated with high diversification rates (see below).

The processes favoring high net rates of species diversification in herbs should be especially strong in desert annuals. Such plants have very short generation times, are almost all animal-pollinated, and lack adaptations for long-distance seed dispersal. Repeated drought and patchy rainfall can create repeated population bottlenecks and extrinsic mating barriers, accelerating genetic differentiation at small spatial scales.

Lewis (1962, 1966) and Raven & Axelrod (1978) proposed that these processes, when combined with selfing ability, can lead to *saltational* (or *catastrophic*) *speciation*, in which chromosomal rearrangments or unique ecological variants are rapidly fixed in a few generations, presumably during a population crash leading to more or less immediate reproductive and ecological isolation. Drastic fluctuations in rainfall and population sizes of annual plants are characteristics of summer-dry, Mediterranean and desert climates in California. The origin of winter rainfall there 15 Ma ago (Baldwin & Sanderson, 1998) may have driven the explosive speciation of desert and vernal-pool annuals in the California Floristic Province, where they comprise over 2000 native species and 26% of all native vascular plants, and include such highly diverse lineages as the tarweed alliance (Madiinae: Asteraceae), *Clarkia, Collinsia, Downingia, Gilia, Lasthenia, Lupinus, Mentzelia, Mimulus, Myosurus, Nama, Nemophila, Phacelia,* and *Streptanthus* (Raven & Axelrod, 1978). A rigorous analysis of these winter-annual lineages is now needed to determine whether they show higher rates of diversification than their perennial sister groups. An initial indication, however, can be gleaned from the phylogeny of Hydrophyllaceae presented by Ferguson (1998). Clade I of that study consists a subclade of ca. 226 species composed almost entirely of annual herbs in the genera *Ellisia, Emmenanthe, Eucrypta, Nemophila, Phacelia, Pholistoma,* and *Romanzoffia,* with a reversion internally to the perennial habit in eight species of *Hydrophyllum,* with all sister to a clade of three species of perennial herbs (*Draperia, Hesperochiron, Tricardia*). Clade II consists of ca. 50 annual species of *Nama* sister to a clade of 17 perennial species of *Eriodictyon, Turricula,* and *Wigandia,* including perennial *Nama lobbii* and *N. rothrockii.* In this single family, acquisition of the annual habit accelerated speciation 3- to 75-fold relative to perennial herbs and/or shrubs.

Stephen A. Smith & Beaulieu (2009) found that herbs accumulate more changes in climatic niche per million years (Ma) than woody plants, as expected given their shorter generation time. Among annual and perennial herbs in *Oenothera* sections *Anogra* and *Kleinia*, especially rapid rates of climatic divergence have occurred, with shifts of up to ±8°C in the average maximum temperature of of the warmest month in the last 0.25 Ma (Evans & al., 2009). Among herbs in the family Onagraceae more generally, sexual forms appear to evolve antiherbivore defenses faster and more effectively than do asexual sister clades (M.T.J. Johnson & al., 2009).

(2) *Plants pollinated by animals vs. wind* (Eriksson & Bremer, 1992; Ricklefs & Renner, 1994; Dodd & al., 1999; Kay & al., 2006). – Wind pollination has evolved at least 65 times across the angiosperms (Linder, 1998), but animal-pollinated lineages have 5.7 times as many species as their wind-pollinated sisters. This pattern, based on 16 contrasting pairs of sister clades across angiosperms (Kay & al., 2006), probably arose because of the greater specificity of mating and reproductive isolation afforded by animal pollinators (V. Grant, 1949, 1981; Dressler, 1981; Schiestl & Schlüter, 2009) and divergent selection for adaptive radiation in pollinators (V. Grant & Grant, 1965; Stebbins, 1974). Given that net diversification repeatedly declines with the transition from animal to wind

pollination, it is logical to infer that the rise of animal pollination at or near the base of the angiosperms played some role in their great diversification (ca. 300,000 species) relative to their largely wind-pollinated sister group, the gymnosperms (ca. 800 species) (Dodd & al., 1999). The fact that net diversification does *not* increase sharply at the base of the angiosperms, in association with the (largely) animal-pollinated angiosperm flower, but at later nodes suggests that the acquisition of animal pollination alone was not *the* key innovation that triggered higher overall rates of net diversification in the angiosperms as a whole (Sanderson & Donoghue, 1994).

Some wind-pollinated plants *can* select their own pollen, in the lab (Niklas, 1985) or in the field (Linder & Midgely, 1996), apparently by creating species-specific patterns of air movement near their extensive, variously shaped stigmatic surfaces. Yet these data also demonstrate "leakage" of 20% to 50% non-self pollen onto stigmas, indicating that—compared with animal-pollinated sister species or nearly isogenic lines (NILS) that differ at a single locus affecting flower color or shape (Schemske & Bradshaw, 1999; Bradshaw & Schemske, 2003)—variation in wind pollination is very unlikely to provide reproductive isolation and thus to trigger rapid speciation.

Wind pollination appears to be favored by open habitats and local plant abundance (Regal, 1982; Linder, 1998; Friedman & Barrett, 2008, 2009) and by tall stature, vigorous vegetative spread, and adaptation to patchy disturbances (Givnish & al., in press). Its evolution is strongly associated with unisexual flowers, loss of nectar and perianth, and small numbers of ovules (Friedman & Barrett, 2008).

(3) *Plants with poorly dispersed seeds, including understory species with fleshy fruits* (Eriksson & Bremer, 1992; Ricklefs & Renner, 1994; Givnish & al., 1995, 2009; Tiffney & Mazer, 1995; Givnish, 1998; J.F. Smith, 2001; Price & Wagner, 2004). – The connection between rapid speciation and fleshy fruits in understory lineages has already been described at length. Seven of the eleven largest angiosperm clades in the Hawaiian archipelago are understory plants dispersed by birds, and avian dispersal is the strongest correlate of species richness among the 28 Hawaiian lineages studied (Price & Wagner, 2004). In eleven of fourteen cases, fleshy-fruited understory clades from the Neotropics had more species than their sister clades with capsular fruits (J.F. Smith, 2001). However, neither Eriksson & Bremer (1992) nor Ricklefs & Renner (1994) differentiated among dispersal of fleshy fruits in forest understories vs. forest canopies, forest gaps, and open habitats and so concluded that there is no net effect of biotic dispersal per se on speciation. Eriksson & Bremer (1991) came closest seeing the relationship between mode of seed dispersal and growth form, noting a positive correlation between species richness and fleshy fruits in shrubby Rubiaceae, but a negative one in tree-like members of the same family. Interestingly, both Eriksson & Bremer (1992) and Tiffney & Mazer (1995) found a positive relationship of abiotic dispersal to species richness in herbaceous families, and a negative relationship in woody families. Arguably, the greater number of species in herbaceous lineages with abiotic vs. biotic dispersal might reflect the largely open habitats of such lineages and the expected greater dispersibility

of fleshy fruits in such habitats. The cause of the negative relationship of abiotic dispersal to woody diversity is, however, enigmatic. Although no formal analyses have been conducted to evaluate the impact of seed mass on diversification, Givnish & al. (2009) argued that low diversification rates seen in Hawaiian lobeliads from open, windswept, high-elevation habitats reflected the excellent dispersal of their tiny, wind-dispersed seeds, and that the intermediate levels of diversification seen in fleshy-fruited lineages from open habitats reflects their greater dispersibility than understory *Cyanea*. It should also be noted that several lineages with unusually heavy seeds—including many genera (e.g., *Dipterocarpus, Hopea, Shorea, Vatica*) of Dipterocarpaceae, *Quercus, Castanopsis*, and *Lithocarpus* of Fagaceae, and *Banksia/Dryandra* and *Hakea* in Proteaceae among woody plants—have large numbers of present-day species, often endemic to narrow areas. The ruschioid Aizoaceae of South Africa, including the "stone plants" and numerous other succulents of the semi-arid Karroone, and one of the most rapidly diverging groups of angiosperms documented to date (0.77 to 1.75 Ma^{-1} [Klak & al., 2004]), all have tiny seeds. However, these lack dormancy and are splash-dispersed from hygrochastic capsules under wet conditions, resulting in exceptionally limited seed dispersal (ca. 1 m) (Hartmann, 1978; Linder, 1985; Ihlenfeldt, 1994; Parolin, 2001; Ellis & al., 2006). Diversification in this group appears to involve early, rapid adaptive divergence based on soils and flowering time, followed by repeated speciation based on limited dispersal (Desmet & al., 1998; Klak & al., 2004; Ellis & Weis, 2006; Ellis & al., 2006). Key innovations—including wide-band tracheids and cylindrical or trigonal leaf cross-sections—that reduce the impact of drought may have also played a role in fostering rapid diversification in this group (Klak & al., 2004).

Seed dispersal via ants is associated with greater rates of net diversification than other modes of seed dispersal seen in sister groups (Lengyel & al., 2009). Ants move seeds over very short distances, with 1 m being the average across many studies (Gomez & Espadaler, 1998), facilitating local genetic differentiation within species (Kalisz & al., 2001; Zhou & al., 2007) and—ultimately—speciation. Myrmecochory may also increase fitness by dispersing seeds to microsites protected from fires, drought, or predators, or fertilized with nutrients derived from the ant nest.

(4) *Families with both woody and herbaceous members, species pollinated biotically and abiotically, species dispersed biotically and abiotically, and species that, in aggregate, have a wide geographic distribution and occur in both temperate and tropical areas vs. those with lesser evolutionary lability* (Ricklefs & Renner, 1994). – Ricklefs & Renner (1994) concluded that phenotypic/ecological "flexibility" is the single most important trait promoting diversification at the family level. Davies & al. (2004a) also found that greater within-family variation in growth form, pollination mechanism, dispersal mode, geographic distribution, and ploidy characterized families that are more species-rich than their sister groups. In some sense, these patterns could simply reflect adaptive radiation, and thus make a legitimate contribution to familial diversity. However, Dodd & al. (1999) argued that these patterns are a

sampling artifacts; a greater range of traits within a family is a consequence of a greater number of species, not vice versa. This inference is supported by Ricklefs & Renner's (1994) own finding that families with both modes of seed dispersal have 14–15 times as many species as those with only biotic or abiotic dispersal. If this pattern were simply a result of adaptive radiation, however, at most a doubling of species would be expected. Ricklefs & Renner (2000) softened their claim somewhat, based on showing that the probability of a lineage proliferating upon arrival in Hawaii has no relationship to the extent of character-state variability within its family. They strongly maintained their view, however, that high species numbers and wide distributions are closely tied.

(5) *Families at lower vs. higher latitudes* (Davies & al., 2004b). – Two theories aim to explain latitudinal gradients in diversity based on energy input to ecosystems. The "greater biomass" theory argues that more energy can support more biomass per unit area, supporting more individuals and, thus, more species (Currie, 1991; Willig & al., 2003). The "faster evolution" theory holds that greater energy inputs should accelerate evolution and speciation by increasing mutation or reducing generation times (Rohde, 1992; Allen & al., 2002). The "greater biomass" theory is dubious; many ecologists have shown that local plant diversity first rises, then falls with productivity (e.g., Whittaker, 1960 for species number vs. rainfall in the Siskiyou Mountains, associated with decreasing canopy cover and increased stratification toward drier habitats, with similar patterns observed in southwestern Australia by Rice & Westoby, 1983). Similarly, Grime (1979) found that temperate herb richness rose, then fell with herb biomass. Other ecologists have found that species richness declines monotonically toward more productive sites (e.g., Tilman, 1982 for drops in grassland diversity with increasing N fertilization). The "greater biomass" theory may apply to the tallest plants with the greatest energy requirements; Currie & Paquin (1987) successfully applied it to trees in North America. Davies & al. (2004b) supported the "greater biomass" theory by regressing various proxies of energy input against species number, with the total range of a family entered as a covariate. Their conclusion, however, should simply be seen as confirming a positive effect of lower latitude and its many correlates (e.g., a history of less dramatic climatic shifts; greater area for ecologically comparable habitats; frost- and glaciation-free habitats) on species richness. Davies & al. (2004b) observed a close correlation of energy input to species richness and to rates of molecular evolution across latitudes, but found no direct tie of species richness to the latter, working against the "faster evolution" model as a driver of species diversification. Ricklefs (1989) argued that much of the drop in tree diversity from tropical to temperate latitudes resides at the familial level, rather than within families, reflecting the fact that few families ever broke the "frost barrier" (see Donoghue, 2008); this has little to do with any of the classic energy-diversity hypotheses. Similarly, Fine & Ree (2006) found that much of the variation in tree species richness from boreal to tropical latitudes on each continent reflects a time-integrated effect of the areas at such latitudes since the Eocene, Oligocene, and Miocene. Terborgh (1973)

argued that greater land area at lower latitudes on a globe, together with greater climatic stability, was largely responsible for latitudinal gradients in plant diversity, but his attempt to account for other patterns based on age and area (e.g., greater diversity on serpentine vs. diorite soils in the Siskiyous) overlooked effects of climate and substrate on stratification and addition of species-rich lower layers to forests and woodlands.

(6) *Families with higher vs. lower rates of genetic divergence* (Barraclough & Savolainen, 2001). – Branch lengths were derived from the three-gene phylogeny of angiosperms based on sequences of plastid *rbcL* and *atpB*, and nuclear ribosomal 18S (D.E. Soltis & al., 2000). Counter to expectations, relative rates of net diversification in sister families rose significantly only with the rates of synonymous (silent) base substitutions, and not with non-synonymous substitutions or morphological change. The latter two rates were positively correlated with each other. Barraclough & Savolainen (2001) argued that these results could reflect variation in generation times, population sizes, or mutation rates among lineages; variation in gene flow and spatial scales of genetic differentiation within species should be added as a possibility.

(7) *Hermaphroditic or monoecious clades vs. dioecious clades* (Heilbuth, 2000; Kay & al., 2006). – Extinction may be higher in dioecious lineages because only half the individuals in a population can set seed. Dioecious populations also have smaller effective population sizes, and can also go extinct due to drift eliminating males or females locally. In addition, the small, unspecialized flowers associated with dioecy does not permit much scope for ecological speciation based on selection for divergent flowers. This argument, however, should also apply to monoecious plants. Interestingly, the fraction of dioecious species in the native Hawaiian flora increases toward older islands, from 13% on Hawai'i and Maui Nui (including Maui, Moloka'i, Lana'i, and Kaho'olawe, joined during the lower sea levels of the Pleistocene), 17% on O'ahu, and 20% on Kaua'i; the incidence of gynodioecy and woodiness (correlated with dioecy and gynodioecy) also increases toward older islands (Sakai & al., 1995). I believe that these patterns, which run counter to trends in net species diversification rates, might reflect an advantage of dioecious or gynodioecious species—which often are woody and have small, visually inconspicuous flowers and fleshy fruits—in shadier, less frequently disturbed habitats on older islands that lack volcanism and have less *Metrosideros* dieback, based on synchronous cohort establishment on new lava flows or the sudden transition to poorly drained soils on young surfaces as fine particles accumulate after those flows (see Akashi & Mueller-Dombois, 1995).

(8) *Early- vs. late-maturing plants among woody angiosperms* (Verdú, 2002). – Presumably this effect is due to the shortening of the life cycle and increasing rates of molecular divergence; increases in the latter are associated with shorter life-cycles or more rapid growth (Gaut & al., 1992; Givnish & al., 2007; S.A. Smith & Donoghue, 2008).

(9) *Plants with bilateral vs. radial flowers* (Sargent, 2004). – Bilateral floral symmetry enforces a narrower range of approaches by pollinators, resulting in a more precise placement of pollen, and facilitating the evolution of a diversity of reproductively isolated species that partition the same pollinator(s) through differential pollen placement (Neal & al., 1998).

(10) *Plants with nectar spurs vs. those without such spurs* (Hodges & Arnold, 1995; Ree, 2005; Cacho & al., 2010). – See discussion above under Sexual selection.

(11) *Plants pollinated by hummingbirds vs. other pollinators* (Gentry, 1982; Kay & al., 2005; Schmidt-Lebuhn & al., 2007; Givnish & al., in prep.). – Schmidt-Lebuhn & al. (2007) found that, in five of six comparisons, hummingbird-pollinated lineages had higher rates of diversification than sister lineages. Givnish & al. (in prep.) add that, among bromeliads, the mostly hummingbird-pollinated Pitcairnioideae-Bromelioideae-Puyoideae (ca. 1300 spp.) has ca. 13 times as many species as its insect-pollinated sister Navioideae. The cause of higher diversification rates in hummingbird-pollinated lineages is unclear (see Castellanos & al., 2003; Schmidt-Lebuhn & al., 2007), but association with the continued uplift of the northern Andes and climatic oscillations during the Pliocene-Pleistocene, as well as the rapid evolution there of more than 300 recently derived hummingbird species may have been important (Gentry, 1982; Graham, 1997; Kay & al., 2005). Hummingbird pollination may directly accelerate speciation by favoring the origin of gullet-shaped flowers from ancestral cup-shaped flowers. Once such narrow, exclusionary blossoms appear, their length and shape could easily be adjusted to attract hummingbird species with different bill lengths and shapes, providing a ready and rapidly evolved means of pre-mating isolation (Givnish & al., in prep.). Many bird-pollinated lineages (e.g., Gesneriaceae, Lobeliaceae, some Bromeliaceae) also have flowers with bilateral symmetry (see above).

(12) *Latex-bearing clades vs. those without latex* (Farrell & al., 1991). – As an early stage of the coevolutionary herbivore-plant arms race (Ehrlich & Raven, 1964), possession of latex or resin canals should increase plant speciation and reduce extinction by protecting against a variety of herbivores.

(13) *Milkweeds with lower vs. higher concentrations of latex and cardenolides, and higher allocation to alternative defenses* (Agrawal & al., 2009a). – The authors argue that this paradoxical pattern might arise because most herbivores on *Asclepias* are highly specialized, and rather unaffected by latex and cardenolides. By decreasing allocation to latex and cardenolides, current *Asclepias* species have reallocated energy to alternative defenses (e.g., phenolics), spurring a new round of coevolutionary diversification (Agrawal & al., 2009b).

(14) *Epiphytic vs. terrestrial bromeliads, and bromeliad lineages differentiating along geographically extensive, climatically complex, and topographically dissected cordilleras* (i.e., the Andes and the Serra do Mar in southeastern Brazil) (Givnish & al., in prep.). – Several plant traits and habitat features are associated with the rise of epiphytism in bromeliads. Of these, the tank habit, absorptive trichomes, entangling seeds or fruits with moderate dispersal capacity, hummingbird pollination, and (especially) diversification in recently uplifted, extensive montane regions with relatively fertile substrates (i.e., the Andes and the Serra do Mar along the southeast Brazilian coast) show a significant correlation with net species diversification

at the subfamilial level (Givnish & al., in prep.). Limited seed movement coupled with occasional long-distance dispersal can permit allopatric speciation and adaptive radiation to proceed rapidly, and in parallel, in montane habitats along the length of cordilleras dissected repeatedly by drier valleys. Recently uplifted mountain chains, as newly formed, ecologically empty slates, should allow several lineages to diversify within them, irrespective of life form (Benzing, 1990; Linder, 2008). The Andean and Serra do Mar orogenies—with their recently formed montane habitats and numerous external barriers to gene flow, and highly dynamic climates and landscapes during the Pliocene and Pleistocene (Gentry, 1982; Berry, 1989; Van der Hammen, 1995; Gregory-Wodzicki, 2000; Garzione & al., 2008)—do indeed support several diverse plant groups that are widely distributed in each region. Examples include *Calceolaria*, *Centropogon-Burmeistera*, *Epidendrum*, *Espeletia*, *Fuchsia*, *Pleurothallis*, and *Puya* in the Andes, and Asteraceae (*Lychnophora*), Bromeliaceae-Bromelioideae, Eriocaulaceae (*Leiothrix*, *Paepalanthus*), Gentianaceae, Myrtaceae, and Velloziaceae in the Serra do Mar (Gentry, 1982; Prance, 1987; Luteyn, 2002; Young & al., 2002; Knox & al., 2008; Alves & Kolbeck, 2010; Jabaily & Sytsma, 2010). Several clades with the highest rates of net diversification known in plants occur in the Andes, including the current rate champion, heavy-seeded, gravity- or rodent-dispersed Andean *Lupinus* (2.49–3.79 Ma^{-1} [Hughes & Eastwood, 2006]), as well as Andean *Valeriana* (1.71–3.2 Ma^{-1} [Bell & Donoghue, 2005]), Neotropical *Costus* (0.6–2.6 Ma^{-1} [Kay & al., 2005]), Andean *Astragalus* (2.01–2.07 Ma^{-1} [Scherson & al., 2008]), and the mainly Andean higher tillandsioids (0.48–0.68 Ma^{-1} [Givnish & al., in prep.]). Tank-epiphytic bromelioids of the Serra do Mar and nearby areas have the highest diversification rate in bromeliads (1.52–1.73 Ma^{-1} [Givnish & al., in prep.]). These diversification rates are comparable to those for the fastest adaptive radiations on islands, including the Hawaiian silversword alliance (0.56 Ma^{-1} [Baldwin & Sanderson, 1998]), Macaronesian *Sideritis* and *Echium* (0.79 and 0.60 Ma^{-1} [Kim & al., 2008]), and Hawaiian *Cyanea* (maximum rates of 1.36 to 2.09 Ma^{-1} [Givnish & al., 2009]).

(15) *Epiphytic vs. terrestrial orchids* (Gravendeel & al., 2004; Silvera & al., 2009). – Orchid subfamily Epidendroideae is composed mainly of epiphytes and contains 80% of the estimated 25,000 species of orchids worldwide. Its sister, subfamily Orchidoideae, contains only one fifth as many species and is almost entirely terrestrial. Gravendeel & al. (2004) showed that, based on a random sample of 100 orchid genera, epiphytic genera had significantly more species than terrestrial genera ($P < 0.01$). Gentry & Dodson (1987) argued that epiphytism in montane forests should stimulate speciation because (1) bark surface is far greater than ground surface, and can thus support more plants and species; (2) epiphytes can finely partition the substantial environmental gradient from brightly lit, low-humidity twig tips to densely shaded, highly humid boles; and (3) in orchids, a high degree of specialization on individual pollinators can also drive speciation. Silvera & al. (2009) suggested that the origin of CAM photosynthesis in association with epiphytism should accelerate speciation by (4) providing access to new, highly xeric microsites. Benzing

(1990) proposed that (5) recently uplifted mountain chains provide an ecologically open slate with numerous extrinsic barriers to dispersal; this, combined with the invasion of a novel range of epiphytic microhabitats, should foster explosive speciation. Twig epiphytes, adapted to life on the outermost branches of host canopies, have a very short generation time (<2 years) and hence (6) should speciate rapidly (Chase & Palmer, 1997; Benzing, 1990). Silvera & al. (2009) found support for CAM accelerating diversification, but an even strong association between epiphytism and diversification. Gravendeel & al. (2004) found support for repeated bursts of speciation associated with multiple origins of the twig-epiphyte habit, but no support for the pollinator-specialization hypothesis.

The last conclusion seems unlikely to be correct. First, it is directly contradicted by the findings of Schiestl & Schlüter (2009). Second, hard pollinia with sticky viscidia—characteristic of epidendroids—can permit precise placement of pollen on floral visitors, allowing specialization on individual pollinators or parts of individual pollinators, which should lead readily to divergent selection and ecological speciation (Dressler, 1981). Third, in a survey of several Bangladeshi orchids, Huda & Wilcock (2008) found that fruit set is lower in species with smaller populations, smaller inflorescences, self-incompatibility, and non-sectile pollinia. Each of these traits—and thus, small effective population size—is associated with epiphytism, as are exceptionally large and showy flowers. Consequently, intermittent genetic drift may be more important in epiphytes, and alternate with strong selection on floral traits. Such conditions should lead to rapid speciation, especially if combined with short lifecycles, based on previous general arguments made by Tremblay & al. (2005). Lower fruit set and small effective population size in sexually deceptive orchids, together with the massive effects of minor changes in floral attractants (Salzmann & al., 2006), may be responsible for the high rates of speciation in such orchids as well (see Cozzolino & Widmer, 2005).

(16) *Young vs. old lineages* (Magallón & Castillo, 2009). – Although this would appear to be the most general finding emerging from the recent literature (Fig. 9A), and consistent with the idea that rates of adaptive radiation should be fastest early during the history of individual groups, there is strong reason to believe that it is, at least in part, a statistical artifact. Regardless of whether pure-birth, or mixed birth-death processes, are used to model net diversification rates, ultimately all such calculations depend on comparing ln S with t, where S is the number of the current species in a lineage and t is the stem age of that lineage. For pure-birth models, (ln S) / t is the diversification rate D. Based on the data presented by Magallón & Castillo (2009), there is a strong negative relationship between diversification rate and stem age using a phylogenetically unstructured analysis:

$$D = 30.74 t^{-1.37} \qquad (2)$$

($r^2 = 0.268$, $P < 0.0001$ for 2-tailed t-test with 67 d.f.). However, this estimate is clearly inflated by autoregression, given that it involves plotting (ln S) / t vs. t. Essentially, this can be seen

as regressing A / t vs. t, where A is random variable and the expected power-law fit is $D = kt^{-1.0}$, where k is a constant. A bias-free estimate of diversification rates can be obtained by instead plotting S or ln S vs. t (e.g., Fig. 3A). However, the best-fit regressions across angiosperms using linear, logarithmic, exponential, or power-law models for S vs. t are not significant ($P > 0.12$); the same is true for ln S vs. t ($P > 0.22$). (Fig. 9B–C). The best-fit models for ln S vs. t explain only 1.1 to 2.4% of the variance in D—or 4.0% to 8.8% of that explained by equation (2)—implying that 91.2% to 96.0% of the fit may be illusory and a result of autoregression. As Ricklefs & Renner (1994) noted for their sample of angiosperm families, there is no relationship between age and species richness; the same is true for the ordinal data compiled by Magallón & Castillo (2009). Species richness per clade, in other words, appears—at least at first glance—to be a random variable with respect to stem age. This key finding—which could reflect decreasing rates of diversification within lineages as they fill the available ecological space, among many possibilities—suggests that ecological or historical constraints on the volume of that space might, in many instances, be more important than diversification rate in determining patterns of species richness (e.g., see Ricklefs, 2006, 2010; Ricklefs & al., 2007).

The possibly artifactual nature of a relationship between apparent diversification rate and age of clade could have wide-ranging implications, extending far beyond plants. All of the highest rates of net diversification known across organisms are for young clades (e.g., 2.93 Ma^{-1} for Bermin *Tilapia*, 6.1 Ma^{-1} for Malawi *Astatotilapia*, and 178.8 Ma^{-1} for Natron *Oreochromis*, with stem ages of 0.75 Ma, 1.00 Ma, and 0.009 Ma (see data of Seehausen, 2006).

More generally, all models for net diversification assume continued rates of exponential growth in the numbers of species per lineage. If there are ecological constraints on the numbers of species per lineage, then calculations of net diversification rates are subject to massive biases, unless they are instantaneous estimates based on inferred rates of cladogenesis through time for ancestors of surviving taxa (Rabosky & Lovette, 2008; Rabosky, 2009a,b). For example, if one ignored ecological saturation of net speciation and repeated parallel radiation on individual major islands in *Cyanea*, then one would estimate a net diversification rate $D = 0.37$ Ma^{-1}. If one instead takes these factors into account, a far higher rate of up to 2.09 Ma^{-1} emerges (Givnish & al., 2009).

Several of the preceding patterns confirm long-held theories re the effects of growth form, longevity, dispersal, and floral evolution on diversification. The strongest effects seem to be associated with limited seed dispersal and its synergistic effects with adaptive radiation and ecological speciation (e.g., Patterson & Givnish, 2004; Hughes & Eastwood, 2006). Surprisingly, as yet there is little general support for the diversifying effect on plants of coevolution (i.e., "escape and radiate") between plants and herbivores hypothesized by Ehrlich & Raven (1964). Several very important papers have recently established that link for herbivore diversification, showing, for example, that (1) "solving" the glucosinolate defense led to a large increase in diversification among Pierinae butterfly
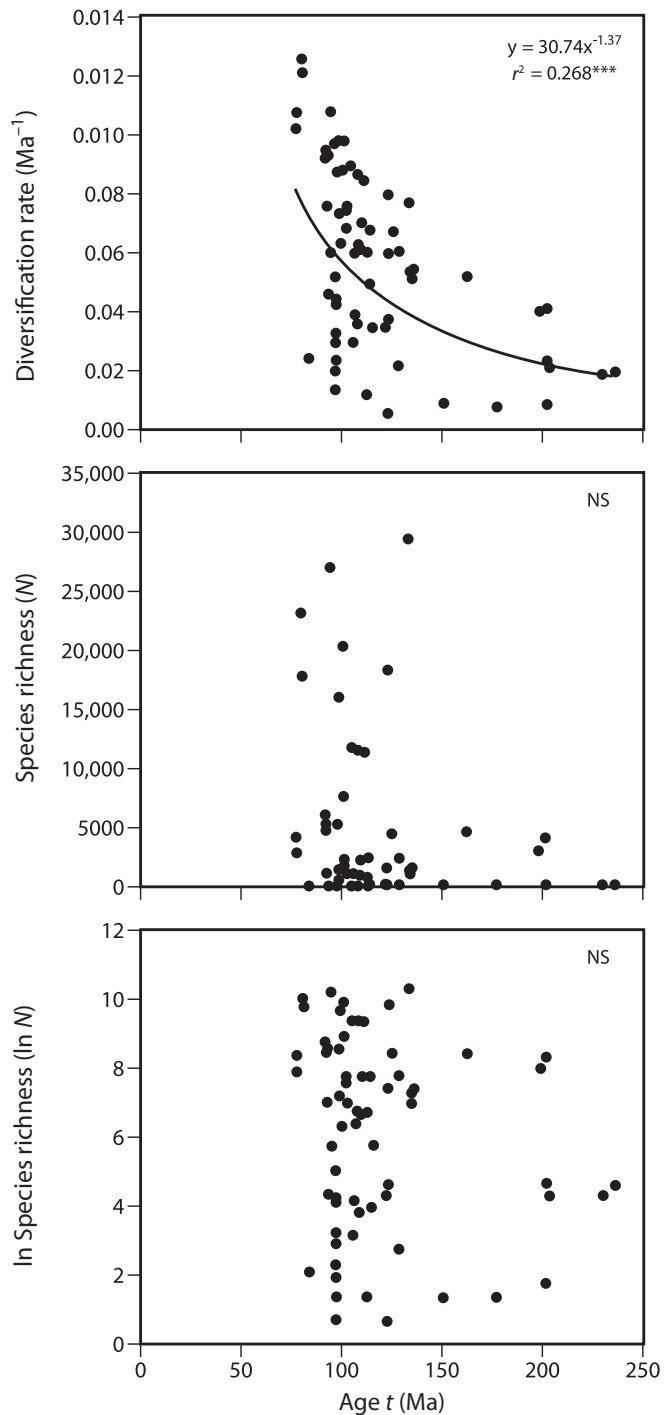

Fig. 9. A, Apparent rate of net species diversification for all orders of angiosperms with more than one surviving species, assuming pure-birth process ($D = (\ln N) / t$), plotted against stem age t; monotypic *Amborella*, *Desfontainia*, and *Paracryphia* were excluded. Data from Magallón and Castillo (2009). Curve indicates significant exponential decline of D with t. However, this pattern appears to be artifactual, a result of plotting A / t vs. t, where A is a random variable (see text). Confirming this, I found no significant relationship between t and **(B)** N or **(C)** ln N.

larvae shortly after the origin of that defense in the Brassicales (Wheat & al., 2007); (2) five independent invasions of novel, asterid food-plant lineages accelerated diversification in *Phytomyza* leaf miners (Winkler & al., 2009); and (3) shifts to crown-group angiosperms and (especially) to monocots and eudicots soon led to massive pulses of diversification in herbivorous weevils (Curculionidae), one of the most diverse lineages of insects (McKenna & al., 2009). These papers follow on others showing a general increase in insect diversity associated with herbivory (Mitter & al., 1988; Farrell, 1998; Farrell & Sequeira, 2004). Studies of this kind, aimed at diversification of their angiosperm hosts, are now needed. It is intriguing that locally co-occuring species of the large genus *Inga* (Fabaceae) are more divergent in their anti-herbivore defenses than would be expected at random, suggesting that selection and competitive sorting have favored divergence in these important features (Kursar & al., 2009). Agrawal & al. (2009b) and Becerra & al. (2009) have also shown, using *Asclepias* and *Bursera*, respectively, the theoretically expected pattern of escalation of plant defenses over time.

Plant-animal coevolution—whether involving plants and herbivores, plants and pollinators, or plants and seed dispersers—may well have helped trigger the massive diversification of the angiosperms, even if general support for arms' races triggering high net rates of diversification is, as yet, lacking. As expected, the faunal similarity of insect communities on different species of tropical tree species decreases with phylogenetic distance between those hosts (Weiblen & al., 2006). Recent evidence suggests that the initial surge of diversification in flowering plants corresponds to the evolution of photosynthetic rates much higher than their gymnosperm and fern competitors, associated with substantial increases in leaf vein density, and thus leaf (and, presumably, stem) hydraulic conductance (Boyce & al., 2009; Brodribb & Feild, 2010). Economic defense theory (Coley, 1983; Coley & al., 1985) predicts that increases in photosynthetic rate should favor abandoning massive outlays in quantitative defenses (e.g., tannins, phenols). Did this strategy—coupled with the three- to four-fold rise in angiosperm photosynthetic rates early in their evolution (between 140 and 100 Ma ago)—in turn favor the evolution of qualitative defenses (e.g., alkaloids, cardenolides, glucosinolates, effective against most but not all herbivores at concentrations <0.1% of plant mass) and thus trigger the enduring arms-race between angiosperms and their herbivores, leading to the huge diversity of angiosperms and insects we see today? Does the higher rate of photosynthesis in herbs help account for the widespread occurrence of qualitative toxins in them, or for their more rapid rate of speciation than woody plants? Answers to these two questions may provide some very deep insights into the basis of angiosperm and insect diversity.

Overall species richness. — In recent years, important evidence has emerged that local and regional plant species richness is indeed predictable. For example, woody plant diversity per 0.1 hectare increases with rainfall (and thus, with decreasing seasonality) in the Neotropics in a highly regular fashion (Gentry, 1982, 1988; Givnish, 1999; Phillips & Miller, 2002) (Fig. 10). Givnish (1999) argued that this striking pattern is

generated by (1) increases in the intensity of density-dependent mortality toward rainier sites, based on the desiccation intolerance of many natural enemies of plants (i.e., small-bodied insects, fungi, nematodes); (2) increased stratification, due to many more small stems in rainier sites, reflecting lower whole-plant compensation points and/or increased toppling of trees on sodden substrates; and (3) increased speciation in understory plants, associated with their possession of fleshy fruits.

More generally, Kreft & Jetz (2007) were able to account for ca. 70% of global variation in plant species richness of 1032 mainland geographic regions based on a model including *area*, *potential evapotranspiration* (a proxy for latitude and solar energy input), *number of wet days* (a proxy for rainfall and seasonality), *topographic heterogeneity*, and *vegetation stratification* (Fig. 11). At the kingdom level, only the Cape flora showed
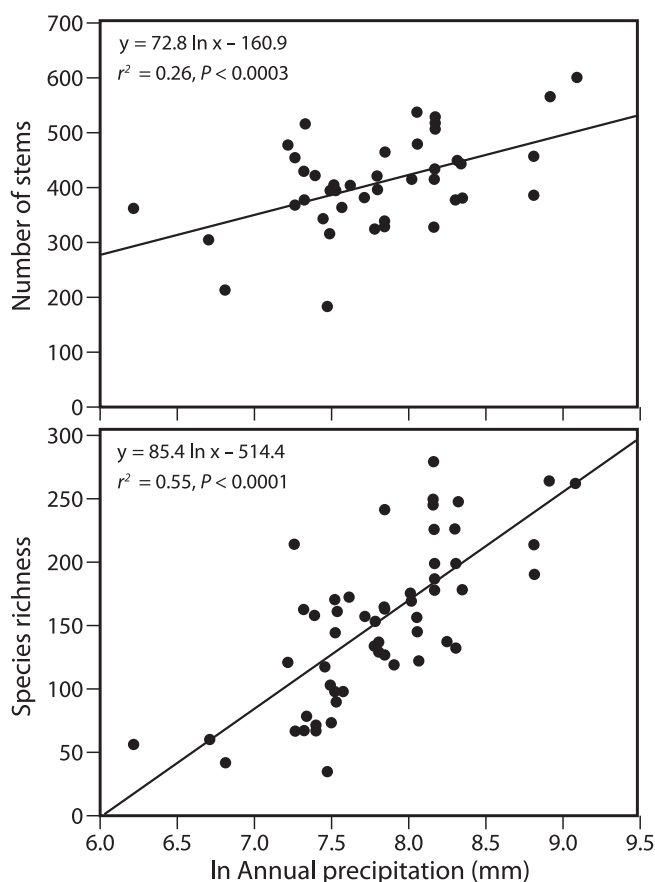

Fig. 10. Significant increases in **(A)** density of woody stems >2.5 cm dbh per 0.1 ha and **(B)** number of woody species as a function of annual precipitation in Neotropical forests (redrawn from Givnish, 1999, based on data from Gentry, 1982). The rise in woody stem density in almost entirely due to a large increase in the number of small stems <10 cm dbh, probably reflecting an increase in whole-plant shade tolerance due to greater supply, or an increase in understory light supply due to more tree toppling on sodden soils. The observed increase in the number of woody species with annual rainfall, however, cannot be explained entirely by the increased number of understory stems, and instead may represent greater attack by small-bodied, desiccation-intolerant specialist plant enemies (e.g., insects, nematodes, fungi) (Givnish, 1999).

a significant excess of species richness, with more than twice as many species (9000 species in 90,000 km^2) as would be expected from its area and environmental characteristics. Several authors have attempted to account for the exceptional plant diversity of the Cape Floristic Province, invoking a relatively stable Pleistocene climate and extensive topographic relief, soil diversity, adaptive radiation in pollination syndromes and fire-survival strategies, as well as limited seed-dispersal distances (see Linder, 1985, 2003, 2006; Cowling, 1990; Cowling & al., 1992; Goldblatt & Manning, 1996, 2002; S.D. Johnson, 1996, 2006; Verboom & al., 2004, 2009; L.A. Johnson & al., 2008; Nicotra & al., 2008; Van der Niet & Johnson, 2009). Analyses of large Cape genera implicate ecological shifts in 80% of sister-species pairs, with shifts in habit, pollinator, and fire-survival strategies being especially common (Van der Niet & Johnson, 2009). Surprisingly, given the exceptional floristic divergence among soil types, edaphic shifts occurred in only 17% of sister-species pairs. In addition, Van der Niet & Johnson (2009) found little difference in species' range size between the Cape Floristic Province and the adjacent summer-rainfall region. In frequently burnt landscapes, including much of the Cape region, greater local diversity is expected in less productive areas as a result of the slowing of competitive displacement during succession (Huston, 1979; Walker & Peet, 1984), which may partly account for the much higher diversity of Mediterranean scrub in South Africa and southwestern Australia relative to areas with similar climate but richer soils in North and South America as well as the Mediterranean region. In Proteaceae, Sauquet & al. (2009) found that clades in nutrient-poor—and thus fireswept—portions of the Cape Floristic Province and Southwest Australia diversified much more rapidly than in nutrient-rich, fire-poor Chile. Often overlooked, however, is the potential multiplier effect of poor seed dispersal on speciation favored by specialization to different ecological conditions. Linder (1985) and Goldblatt & Manning (2002) noted that few species in the Cape flora had evident adaptations for long-distance seed dispersal. Bond & Slingsby (1983) argued that fleshy fruits adapted for vertebrate dispersal were so rare because plants on sandy soils could not afford to allocate resources to "protein-rich" drupes and berries. Given that such fruits are not, in fact, protein-rich, I would argue that the low "protein subsidy" of caterpillars available to frugivorous birds in well-defended plants on infertile soils is the main impediment to the evolution of fleshy fruits in such habitats, and that poor soils can contribute to plant species richness by retarding seed dispersal in this way (see Givnish, 1998 and above). The Cape flora is also very rich in ant-dispersed species (Bond & Slingsby, 1983), as is that of Southwest Australia (Berg, 1975). Ant dispersal is associated with short dispersal distances and high rates of diversification worldwide (Lengyel & al., 2009).

Kreft & al. (2008) found that the species richness of islands responded to many of the same extrinsic drivers as mainland areas, but that area and isolation—and, to a lesser extent, geology—played a greater role in determining species richness. Their complete model accounts for 85% of the variation in plant species numbers across islands. The ability to predict overall species richness for islands and regions raises the hope that, someday, we will be better able to understand the limits on the species richness and diversification rates of individual groups of plants, why some groups radiate extensively while others do not, and how important ecological constraints on genetic differentiation within species are to the overall pattern, tempo, and spatial scales of plant speciation.

At regional scales within continents, ecological constraints on both diversification rates and species richness may help determine local variation in plant species number. As noted above, catastrophic speciation should be common in desert annuals. Such speciation in herbs might also occur on serpentine soils (Raven & Axelrod, 1978). Few species have evolved adaptations that allow them to tolerate the unusually high Mg : Ca ratio, high levels of sulfate ions, and abundant heavy metals (Kruckeberg, 1984; Rajakaruna & al., 2003). While serpentine
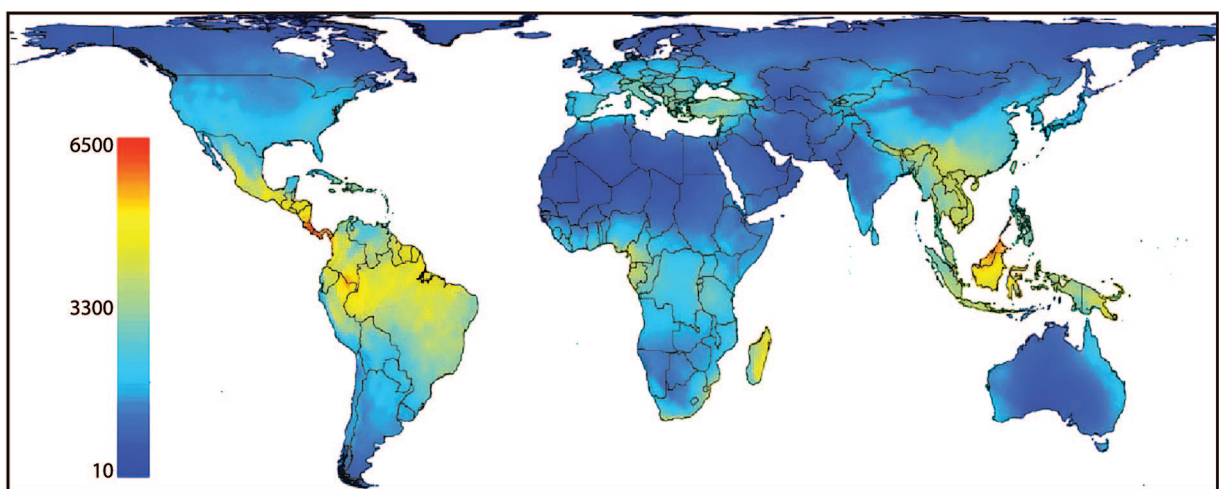

Fig. 11. Regional level of plant species richness predicted by Kreft & Jetz (2007), based on a model incorporating area, potential evapotranspiration, number of rainy days, topographic diversity, stratal complexity of vegetation, and spatial autocorrelation in each of the predictor variables and regional species richness.

outcrops are often sparsely covered with vegetation, due to thin soils and toxicity of the substrate to most plants, sparse cover and the fissured bedrock results in such substrates being "springy" and carrying water at depth. Raven & Axelrod (1978) thus proposed that several widespread plant species became adapted to and invaded serpentine over time, and that rarely catastrophic droughts would extirpate all but the serpentine populations. Subsequent selection and inbreeding within remnant populations would fix serpentine adaptations and traits isolating them reproductively from nearby relatives. The earlier flowering of many serpentine species—associated with open, thin-soiled, rapidly warming habitats—could provide the latter (Rajakaruna, 2004). Although serpentine tolerance could evolve rapidly on widely separated outcrops in this fashion, the rise of serpentine tolerance does not appear to spawn large clades. In California, with the richest serpentine flora of any area worldwide, 215 species of 8000 total are more or less restricted to serpentine, with 89% in the Coast Ranges, and 9% in the Siskiyou/Klamath region; many are isolated species within genera (Kruckeberg, 1984). For example, in *Calochortus*, including >10 serpentine endemics, tolerance evolved seven times in mostly small clades, with tolerance concentrated in two clades near the Bay Area and the Cascades (Patterson & Givnish, 2004: fig. 5c). In *Navarretia*, serpentine tolerance evolved independently in three species; by contrast, invasion of vernal pools and other ephemeral wetlands lead to a massive radiation (Spencer & Porter, 1997). Presumably, the latter reflects the occasional dispersal among such habitats (and not serpentine!) of waterfowl with mud and (otherwise poorly dispersed) seeds on their feet, and rare sheet flow across such habitats.

As expected from the preceding arguments, the most recently divergent species endemic to California are concentrated in the Desert and Great Basin provinces (Kraft & al., 2010), where a large fraction of the flora is composed of annuals. The most narrowly distributed endemics are concentrated in the Coast Ranges and adjacent lowlands, as well as the Sierra Nevada (Kraft & al., 2010), areas of great topographic, climatic, and edaphic complexity, including numerous isolated outcrops of serpentine and—in the lowlands—vernal pools.

The success of models for regional species richness based on ecology and the physical environment must, however, not blind us to the important role of history or other processes in affecting species number. As Ricklefs (2006) has argued, lower rates of extinction during the Pleistocene glaciations and greater topographic and climatic diversity left East Asia with a much greater diversity of temperate deciduous tree genera than western Europe and western and eastern North America, despite all having started with roughly comparable numbers of genera.

■ CONCLUSIONS AND FUTURE DIRECTIONS

Several major themes and suggestions for future research emerge from considering the connections between ecology and speciation in plants. First, limited seed dispersal is an important determinant of the spatial scales of gene flow and genetic differentiation within species, which in turn can be key precursors to speciation. Other things being equal, lineages with more restricted dispersibility should speciate more frequently and at finer spatial scales. Meta-analyses by Kisel & Barraclough (2010) show that the minimum area for in situ speciation does increase with the spatial scale of gene flow in various organisms. Now we need studies to test whether the rates and spatial scales of speciation in various plant lineages increase with the intraspecific spatial scales of gene flow and genetic differentiation in those groups. Especially important would be field tests focusing on clades in which the mechanism and ecology of seed dispersal varies (e.g., the Hawaiian lobeliads), and on comparisons of the rates of diversification and intraspecific scales of gene flow and genetic differentiation in vertebrate- vs. wind-dispersed clades in tropical forest understories and their relatives in forest gaps or open habitats. Coordinated studies of speciation, endemism, and the spatial scale of gene flow across several lineages with large vs. small seeds, and in areas where passive seed dispersal dominates (e.g., California Floristic Province, Cape Floristic Province, tepui summits) might be particularly illuminating.

Second, adaptive radiation clearly helps increase species richness in several plant clades, but—contrary to the definition offered by Schluter (2000)—does not materially affect diversification in others. Future studies need to address testable hypotheses about the relative size of the impact of adaptive radiation on speciation in different lineages, based on their times of origin, local ecological dominance, presence of competitors, spatial extent of environments inhabited, spatial scale of dispersal, and resources present. In the coming years, derivation of molecular phylogenies for all plant lineages on particular islands or archipelagoes (e.g., Hawaii) and rigorous calibration of these against time might yield several new insights, especially if complemented by fossil evidence on the relative abundance of different groups through time. Rigorous null models of community assembly via adaptive radiation or neutral processes are needed to evaluate the causes of the distribution of species across lineages; models that confuse neutrality with complexity (i.e., with the operation of several niche-based deterministic forces, such as the fit to a "neutral" model of the Lambir data on the relative abundance of tropical trees integrated across a soil ecotone by Volkov & al., 2005) must be avoided. The impact on speciation of adaptive radiation in pathogen resistance is an exciting area that needs further exploration. Ricklefs (2010) argues that shared pathogens benign to one host but lethal to a sister species would prevent secondary contact and thus slow diversification. On the other hand, as argued here and by Givnish (1999) and Agrawal & al. (2009a,b), the evolution of specialized pathogens might instead accelerate diversification in host lineages by selecting for immunity to those pathogens, leading to adaptive radiation in the kinds of enemy-free space. Which is the dominant force? Finally, we need more studies on how the tempo of adaptive radiation changes through time as the volume of ecological space occupied by a lineage increases. What is the evidence for ecological saturation? Over what time scales does such saturation occur, and in what circumstances?

Third, ecological speciation in plants may arise through selection for divergence in pollinators, provided that the resulting reproductive barrier is not too leaky and/or is breaking it is associated with a substantial fitness deficit (i.e., due to unattractive flowers of intermediate form). It might be useful, however, to investigate some model cases—such as a species whose range is embedded in that of its putative sister/ancestor, and in which the two taxa differ in pollinators or flowering phenology—to exclude other mechanisms as driving speciation. Even in cases where reproductive isolation is rather easily achieved, due to the simplicity of genetic control over flowers adapted to different pollinators (e.g., *Mimulus cardinalis* and *M. lewisii* [Bradshaw & al., 1995; Schemske & Bradshaw, 1999]), it seems likely that initial divergence will occur in allopatry or peripatry, with subsequent reproductive and ecological reinforcement in secondary sympatry (Coyne & Orr, 2004). Experimental evidence is needed to determine whether divergence in floral form is actually the driver behind speciation, or instead trails shifts in other isolating mechanisms (e.g., differences in habitat) that incidentally select for different kinds of flowers.

Fourth, hybridization clearly plays an important role in plant speciation, as highlighted by a large number of recent studies, especially on *Helianthus* and *Iris*. Given that the likelihood of transgressive hybridization increases with genetic divergence between parental taxa, and that the chance of such an initial mating declines with genetic distance between the parents, one question now needing greater study is how large is the "sweet spot" for hybrid speciation? Is the range of genetic distances over which mating can occur and lead to transgressive gene expression (thus increasing the chance of reproductive and ecological isolation from the parental taxa) relatively small, or is there a wide range of initial genetic divergence that can less to transgressive hybridization and speciation? Given that the chance of polyploid hybrid speciation—for example, through formation of tetraploid hybrids—vis-à-vis homoploid hybridization increases with genetic distance between the parental taxa (Paun & al., 2009), what impact does polyploid formation have on the formation of transgressive homoploid hybrids? Finally, the most interesting area needing further study is the **syngameon hypothesis,** the idea that many bursts of speciation and/or adaptive radiation may be preceded by transgressive hybridization, bringing together genetic variants in two species and increasing the range of phenotypic expression by each in a novel genetic background. Verne Grant (1981) believed that recurrent crossing in hybrid swarms—syngameons—and the resulting genetic and morphological diversity it spawned lay behind the great species diversity of several large genera (e.g., *Aquilegia*, *Gilia*, *Iris*, *Mimulus*, *Pinus*, *Quercus*), and recent research has suggested that syngameons may have played a role in several other adaptive radiations in plant and animal groups. Rigorous reconstructions of hybridization events and analyses of the rates of speciation and phenotypic divergence before and after such events in several lineages are now needed.

Finally, comparative studies suggest that the rates of net species diversification within lineages, and the standing levels of species richness in particular lineages and regions may, in several instances, be predicted based on ecological constraints. The strong negative correlation between apparent rates of net species diversification and clade age appear to be a mirage, caused by autoregressing $(\ln N) / t$ (or its near equivalent for more complex models than simple exponential growth) against t. Furthermore, the absence of a correlation between species number and clade age generally (see above) argues against rates of net diversification being constant, or being an important constraint on species richness. Future studies should evaluate whether the diversification rate within lineages fall through time, as expected, and whether—contrary to the patterns demonstrated here for nine clades on Hawaii—diversification is higher in older clades on a given island or archipelago. It would also be extremely interesting to see whether the total energy invested in chemical defenses per unit leaf mass is inversely related to photosynthetic rate, leaf hydraulic conductance, and diversification rate across early- and late-divergent clades of angiosperms, as proposed here. The fact that a surprisingly high fraction of the variance in the regional number of plant species can be accounted for in terms of ecology does not deny a role to historical contingencies or other non-ecological or non-local processes. The major challenges for the emerging analyses of the causes of patterns in plant diversity at a global scale are to evaluate the relative roles of local ecology, regional ecology, and history in explaining patterns of plant species richness, and to integrate the contributions of ecological processes (e.g., competition, differential shade tolerance, herbivore defense) and evolutionary processes (e.g., rates of genetic differentiation, speciation, and extinction) to the diversity of different life-forms and the role they play in different ecological contexts. Stephen Jay Gould (1989) famously asserted that "a replay of the tape [of life] would lead evolution down a pathway radically different from the road actually taken." However, the repeated evolution of the same forms in the same ecological contexts—e.g., of the six ecomorphs of *Anolis* lizards on the four islands of the Greater Antilles (Losos & al., 1998), of the >20 independent origins of fleshy fruits and net venation in monocots in shady habitats (Givnish & al., 2005), and of dozens of lineages of trees evolving from herbaceous ancestors on islands (Carlquist, 1974; Givnish, 1998)—belie that claim and support a greater role of ecological determinism than historical contingency and unpredictability. Future studies need to examine further the relative roles of ecology, history, and chance in determining local and global patterns in plant diversity.

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