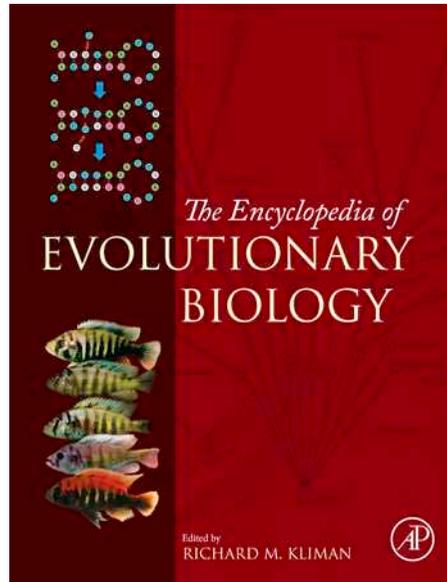


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Convergent Evolution, Adaptive Radiation, and Species Diversification in Plants

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Glossary

Adaptive radiation is the rise of a diversity of ecological roles and associated adaptations within a lineage. Component species of an adaptive radiation often show convergence with ecologically similar members of other lineages.

C₄ photosynthesis is one of three biochemical pathways that plants use to fix CO₂ as reduced carbon (sugar) as food. It has evolved dozens of times from the more common pattern of C₃ carbon fixation, especially in plants of hot, sunny, seasonally dry habitats. C₄ photosynthesis uses PEP carboxylase to capture (carboxylate) CO₂ initially as an organic acid throughout the leaf mesophyll, then ships the acid to cells around each vein bundle, where the CO₂ is released and fixed via light capture and ordinary C₃ photosynthesis in those cells. This spatial separation of CO₂ capture and light capture reduces the inefficiency of photosynthesis caused by the C₃ carboxylating enzyme RUBISCO running photosynthesis in reverse when CO₂ is at low levels inside the leaf. C₃ photosynthesis is often more productive in moist or shady habitats.

CAM (crassulacean acid metabolism) photosynthesis is an unusual photosynthetic variant seen in succulent plants of deserts, as well as in some epiphytes or plants of salt marshes, in which the stomata open only at night, and CO₂ is initially captured as an organic acid; CO₂ is then released from the acid by day and fixed using ordinary C₃ photosynthesis. It greatly reduces water loss but also reduces the total potential amount of carbon fixation.

Convergent evolution = evolutionary convergence is the rise of similarities in form, physiology, and behavior among distantly related organisms that inhabit similar ecological conditions, despite phenotypic differences among their ancestors.

Cordilleras are extensive chain of mountains, such as the Andes or the New Guinea Highlands.

Epiphytes are plants that grown on the branches or trunks of woody plants; the main groups of vascular epiphytes are orchids, bromeliads, ferns, and members of the philodendron family.

Giant rosette shrubs are unbranched or sparsely branched woody plants with large leaves (>20 cm long) clustered around the single terminal bud of each stem; often a dominant growth above treeline in equatorial regions.

Krummholz (crooked or twisted wood in German) is a short, mat-like growth form assumed by some tree species above treeline. These mats can be one to a few tens of centimeters in depth, shelter in the ground boundary layer, and have aerodynamically smooth canopies. In essence, they are gigantic cushion plants. Often they are sheltered under snow during the winter.

Marcescence is the retention of dead organs (e.g., leaves) that would otherwise be shed from stems.

Mycorrhizae are mutualistic associations between plant roots and fungi; the mycorrhizal fungi aid in obtaining water and mineral nutrients, especially phosphorus, from the soil, based the very small diameters and great surface-to-volume ratio of the fungal threads.

Paramo is a distinctive vegetation-type found in the equatorial alpine zone of the Andes in South America, marked by dominance of giant rosette shrubs of *Espeletia* of the daisy family (Asteraceae) and occasionally *Puya* of the bromeliad family (Bromeliaceae). Evergreen, small-leaved shrubs and grasses and sedges are usually also present. A convergent vegetation-type occurs above treeline on the high volcanoes of equatorial East Africa, in the so-called Afro-alpine zone.

Phreatophyte is a plant in a dry region that taps a more or less permanent source of moisture in the underlying water table. Such water tables can be shallow in desert washes, where water carried by floods associated with rainstorms infiltrates the ground, or in low areas in a semi-arid landscape where groundwater can accumulate after flowing from other areas nearby.

Pith is soft, spongy tissue inside plant stems that can act as a storehouse for moisture and nutrients.

Pollinia (singular, pollinium) are discrete packets of hundreds to tens of thousands of pollen grains that are transferred between plants as intact units, attached to pollinators by sticky points of attachment or mechanical yokes. Pollinia have evolved in some orchids and in milkweeds.

Sheet flow is a surface movement of water across nearly flat, relatively smooth soil or rock surfaces in the form of a thin, continuous film or deeper layer or sheet.

Species sorting is the emergence of different distributions of species along an ecological gradient that results from their context-specific advantages in competition, avoiding predation, and/or interacting with mutualists under particular conditions, based on differences in their biological equipment.

Stomatal conductance is a measure of the permeability of the stomata of a leaf to the diffusive movement of water vapor and, thus, of carbon dioxide as well. At a given difference between the humidity (or CO₂ concentration) inside and just outside a leaf, the rate of water loss (or CO₂ uptake) will increase proportionally with stomatal conductance. The latter reflects the density, size, and degree of opening of stomata in a complex fashion.

Vascular plants are those with specialized cells (xylem) that die when mature and act as pipes to conduct water efficiently along the length of a plant, a stem, or a leaf. Vascular plants include the angiosperms (flowering plants), gymnosperms (conifers, cycads, *Ginkgo*, and their allies), and ferns.

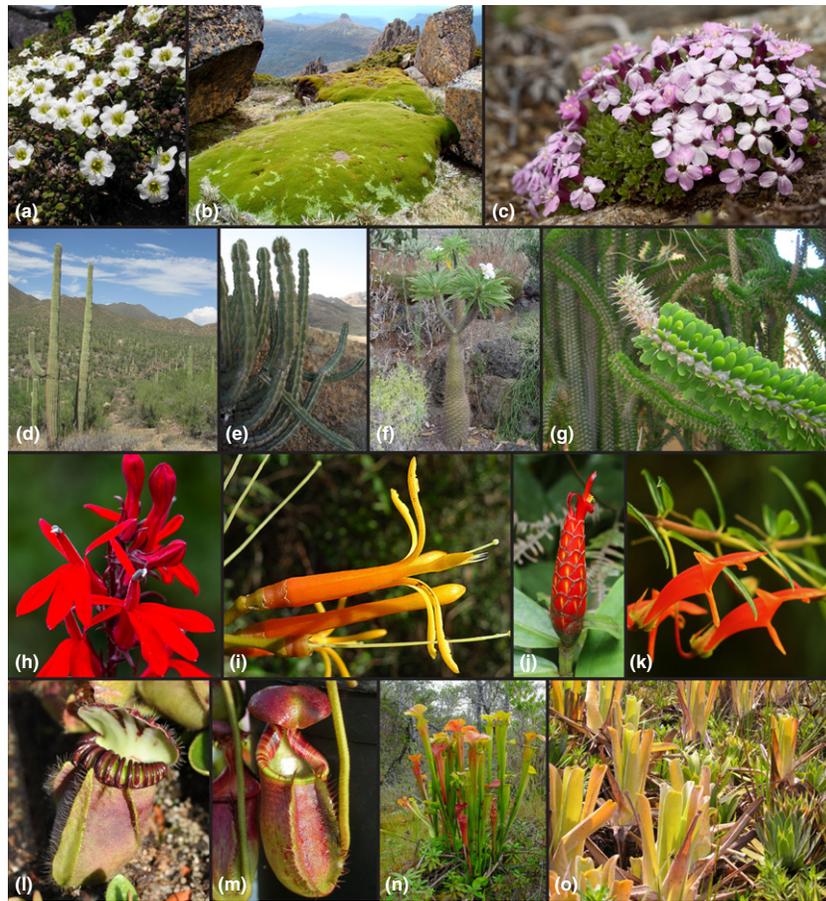


Figure 1 Convergent evolution, exemplified by **alpine cushion plants** ((a) *Diapensia lapponica*, family Diapensiaceae, Mount Chokai, Japan; (b) *Donatia novae-zeelandica*, family Styliaceae, Mount Ossa, Tasmania; (c) *Silene acaulis*, family Caryophyllaceae, near sea level in arctic tundra, Norway); **desert succulent plants** ((d) saguaro (*Carnegiea gigantea*), family Cactaceae, Arizona; (e) *Euphorbia virosa*, family Euphorbiaceae, Namibia; (f) *Pachypodium lamerei*, family Apocynaceae, Madagascar; (g) *Alluaudia procera*, family Didieraceae, Madagascar); **hummingbird-pollinated flowers** ((h) *Lobelia cardinalis*, family Campanulaceae, eastern North America; (i) *Psittacanthus robustus*, family Loranthaceae, Bahia, Brazil; (j) *Costus pulverulentus*, family Costaceae, Costa Rica; (k) *Columnea glabra*, Gesneriaceae, Central America); and **pitfall-trap carnivorous plants** ((l) close-up of small pitcher leaves of *Cephalotus follicularis*, family Cephalotaccaceae, Western Australia; (m) *Nepenthes ephippiata*, Nepenthaceae, Sarawak; (n) *Sarracenia oreophila*, family Sarraceniaceae, southeastern United States; (o) *Brocchinia hechtiioides*, family Bromeliaceae, southern Venezuela).

Evolutionary convergence is the rise of phenotypic similarities among distantly related organisms that inhabit similar ecological conditions. Similar habitats, microsites, or ways of making a living should generate similar selective pressures that, in turn, favor morphological and physiological traits that maximize fitness and competitive ability under those conditions, and lead to convergence among species despite differences among their ancestors. Presumably, this is why alpine plants in so many lineages have a cushion growth form and small, thick leaves; why annuals and succulents with small, silvery, or spiny photosynthetic surfaces dominate so many deserts; and why plants pollinated by hummingbirds tend to have reddish tubular flowers that secrete large amounts of dilute, hexose-rich nectars (Figure 1).

Fitness and competitive ability are context-dependent (Givnish, 1986). The growth forms and traits that maximize success in certain environments (e.g., cushion shrubs with small, thick leaves in alpine and arctic tundra) will almost inevitably be disadvantageous under other conditions (e.g.,

tropical rain forests). Differential adaptation of plant species to one or another set of conditions – and convergent evolution in traits that determine that adaptation – are thus important drivers of plant diversification at large spatial scales. Where physical conditions are key prime determinants of survival and reproduction – as might be expected in extreme environments, in which one or a few conditions are severe or highly unusual and limit the growth and survival of most species – then convergence over evolutionary timescales should be marked. Over shorter periods, local conditions can also allow species to sort themselves along ecological gradients based on their differential ability to survive and compete successfully under different conditions, reflecting differences in their biological equipment. As a result, species sorting – a process operating over relatively short, ecological timescales – can also generate convergence among species at specific points along ecological gradients (Weiher and Keddy, 1995).

Convergence in a particular kind of environment suggests that the trait in question is adaptive there, but functional

studies are required to understand why that trait enhances fitness under those conditions (Givnish, 1997). Concerted convergence – involving two or more genetically, developmentally, and functionally independent traits – can arise through selection pressures imposed by different, correlated features of a given environment. For example, selection for thin broad leaves in forest understories favors net-like venation for biomechanical reasons, while selection for effective seed dispersal in windless understories favors the rise of fleshy fruits. Both traits have arisen, almost always together and associated with the invasion of forest understories, more than 20 times in monocots (Givnish *et al.*, 2005).

Similarities in form and physiology can often lead plants to compete intensely with each other. Consequently, selection and competitive sorting may also favor divergence among locally coexisting species (Stubbs and Wilson, 2004), creating a tension between the amounts of convergence versus divergence expected within a habitat or species assemblage. Divergence may be especially favored under less extreme conditions in which interactions with other plants, rather than the external environment, play a more important role in determining plant survival and reproduction.

Close relatives can often be each other's most potent competitors, based on their phenotypic similarity with each other (e.g., see Burns and Strauss, 2011). Divergent selection among such relatives can lead to adaptive radiation, the rise of a diversity of ecological roles, and attendant adaptations within a lineage (Givnish, 1995; Schluter, 2000). Adaptive radiation is more likely where alternative resources are underutilized by members of other lineages, perhaps as a result of mass extinction, the colonization of isolated islands,

mountains, or lakes by few other groups, or the evolution of a 'key innovation' (e.g., the epiphytic habit) that allows a lineage to invade and ecologically partition a new range of habitats or resources (Givnish, 2015). Adaptive radiation and evolutionary convergence are often two sides of the same evolutionary coin, with species within a radiation adapted to a particular habitat or pollinator class exhibiting convergence with members of other lineages adapted to the same conditions.

Adaptive radiation is often conspicuous in plants on oceanic islands and archipelagoes, with the extent of variation in habitat, growth form, leaf shape, and pollinators being extraordinary in such groups as the Hawaiian lobeliads (Figure 2), mints, silverswords, and *Schiedea* (pink family); *Sonchus* (daisy family), *Echium* (viper bugloss family) and other groups on the Azores, Canary Islands, Madeira, and Cape Verde Islands; and *Scalesia* (daisy family) and *Opuntia* (cactus family) on the Galápagos (Carlquist, 1965; Givnish, 1998; Lindqvist and Albert, 2002; Carlquist *et al.*, 2003; Sakai *et al.*, 2006; Kim *et al.*, 2008; Givnish *et al.*, 2009; Stocklin, 2009). But adaptive radiation can also arise on continents, as exemplified by such groups as mariposa lilies (*Calochortus*, lily family), beardtongues (*Penstemon*, plantain family), and rein-orchids (*Platanthera*, orchid family) in North America (Hapeman and Inouye, 1997; Patterson and Givnish, 2004; Wilson *et al.*, 2007), *Brocchinia* (bromeliad family) in the Guayana Shield (Givnish *et al.*, 1995), lupines (*Lupinus*, legume family) in the Andes, the Brazilian Highlands, and western North America (Drummond *et al.*, 2012), and *Eucalyptus* (myrtle family) and *Banksia* (protea family) in Australia (Williams and Woinarski, 1997; Mast and Givnish,



Figure 2 Adaptive radiation in growth form and habitat in the Hawaiian lobeliads: (a) Giant rosette shrubs in alpine bogs in *Lobelia* sect. *Galeatella*; (b) treelets of wet subalpine openings in *Trematolobelia*; (c) sea cliff succulents in *Brighamia*; (d) canopy trees, exemplified by *Cyanea hamatiflora* (long leaves) in cloud forests on Maui; (e) understory treelets under intact canopies, exemplified by *Cyanea floribunda* on Hawaii; (f) multi-stemmed shrubs of rain- and cloud-forest edges, canopies, and canopies in *Clermontia*; and (g) treelets of mesic scrub in *Delissea* (Givnish *et al.*, 2009).

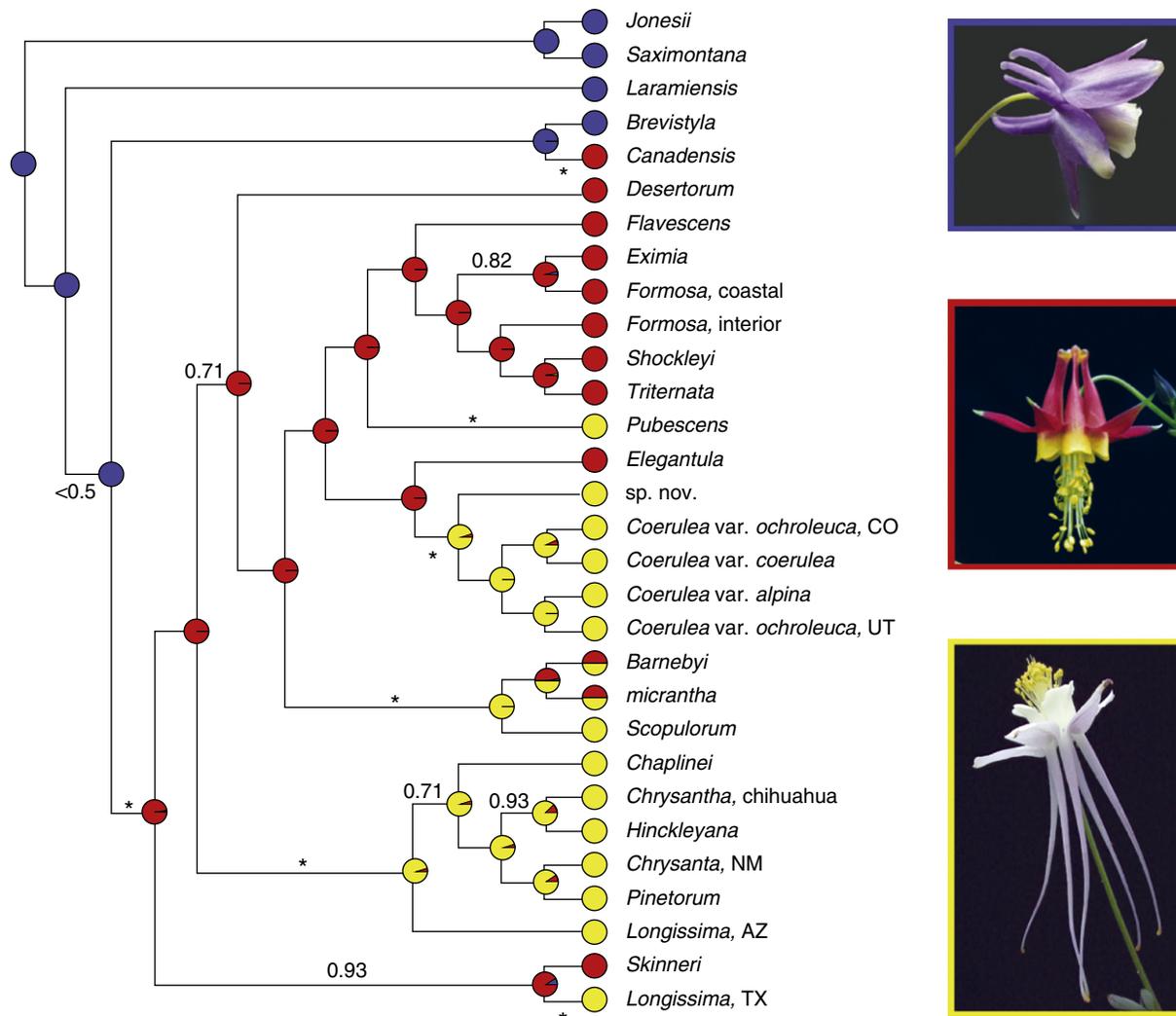


Figure 3 Adaptive radiation involving the sequential evolution of floral adaptations to bumblebees (blue), hummingbirds (red), and hawkmoths (yellow) in North American *Aquilegia*. The probability of each syndrome at each ancestral node is shown by the width of slices in the pie charts. Asterisks indicate inferred shifts in pollinators, including two from bumblebees to hummingbirds, and five from hummingbirds to hawkmoths. All inferred shifts involved an increase in the lengths of floral spurs (containing the nectar) and pollinator mouthparts. Figure from Givnish (2010a), redrawn from Whittall and Hodges (2007).

2002). Given the much wider range of parent materials present on continents versus volcanic or uplifted limestone islands, it is not surprising that adaptive radiation by soil type or bedrock is essentially a continental phenomenon (e.g., invasion of serpentine, gypsum, alkali, clay, loamy, and sandy soils by *Calochortus*, and invasion of serpentine and vernal pools by the pincushion plants (*Navarretia*, phlox family) (Givnish, 2010a)). In the California Floristic Province, over 200 species have become specialized entirely on serpentine soils with aberrant Mg:Ca ratios and high levels of heavy metals (Brady et al., 2005).

Adaptive radiation can lead to increased rates of species diversification within a lineage. Whittall and Hodges (2007) inferred that adaptive radiation in floral form and associated pollinators was a central force driving diversification in columbines (*Aquilegia*) of the Ranunculaceae (buttercup family) (Figure 3). Carlquist (1970) argued that adaptive

radiation in habitat, growth form, and pollinators was a key driver of plant speciation on islands, and Stebbins (1974) made a similar argument for adaptive radiation helping drive the global diversification of angiosperms at the level of families and genera. Set against these ideas, however, is the fact that many lineages exhibit phylogenetic niche conservatism, in which close relatives remain ecologically quite similar and do not appear to undergo adaptive radiation. Crisp et al. (2009), for example, showed that stasis within biomes in plants of the Southern Hemisphere appeared to outweigh biome shifts by more than 25:1 – although this does not exclude the possibility that lineages that remained within a biome have instead radiated with respect to finer-scale variation in habitat, pollinators, seed dispersers, or mycorrhizal fungi. More importantly, there are striking cases of adaptive radiation – for example, Darwin's finches with their great diversity in beak form and diet, and bromeliads in the genus *Brocchinia*, with

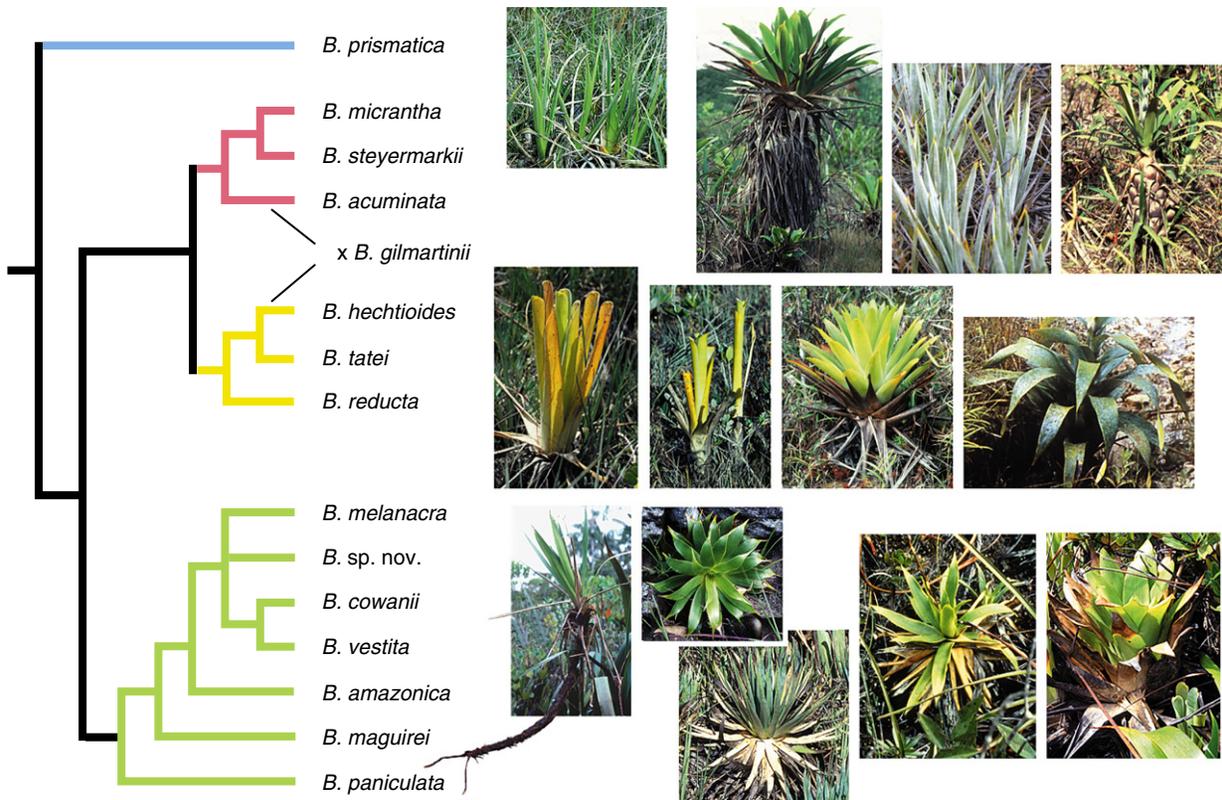


Figure 4 Adaptive radiation in growth form and nutrient capture strategy in *Brocchinia* of the bromeliad family (Bromeliaceae). *B. prismatica* (blue) and all members of the Melanacra Clade (green) except for *B. paniculata* have loosely overlapping leaves, impound no rainwater, have small and sparse leaf hairs (trichomes), and apparently obtain all of their nutrients from bog peats and damp sands and sandstone surfaces. *B. paniculata*, *B. micrantha*, and *B. acuminata* of the Acuminata Clade (red), and all members of the Reducta clade (yellow) have tightly overlapping leaves that form tanks in which rainwater accumulates, and have larger or denser arrays of leaf trichomes. In the Acuminata clade, *B. acuminata* (first image, second row) is a gigantic, unbranched tree-like plant that impounds several liters of water among its leaf bases, in which frogs often live; *B. acuminata* (third image) is an ant-fed plant, with ants living among the swollen, tough, chlorophyll-lacking leaf bases; and *B. steyermarkii* (second image) has lost the tank habit and apparently relies on nutrient absorption via roots from the soil. In the Reducta clade, *B. hechtioides* and *B. reducta* (first and second images, third row) are carnivorous plants, specialized on bees and wasps vs. ants, respectively. *B. tatei* can grow on the ground (as shown in the third image) or as an epiphyte, and catches falling plant debris; terrestrial populations have been seen with N-fixing cyanobacteria growing in their tanks. *B. gilmartinii* (last image, third row) apparently is a hybrid between *B. acuminata* and *B. hechtioides*; its ecology remains uninvestigated. *B. paniculata* (last image, last row) has a growth form similar to that of *B. micrantha*; the remaining species obtain mineral nutrients from the soil. The tough leaf tips of *B. melanacra* (first image, last row), a bog species, are non-functional in fully expanded leaves but protect the terminal bud from fire when young. Phylogeny and images from Givnish *et al.* (1997).

their greater range of strategies for nutrient capture than any other plant genus (Figure 4) – that show either the same rate of species diversification as close relatives, or a much lower rate (Givnish, 2015). Other factors – notably short generation times, and limited seed dispersal leading to genetic differentiation within species at small spatial scales and, ultimately, speciation – can have a profound effect on species diversification independent of ecological divergence among relatives.

Based on the phylogenies (family trees) of various plant lineages derived from DNA sequences and calibrated against time using fossils, comparisons show that the rates of net species diversification tend to be higher in herbs (especially annuals) than in woody plants, in animal- versus wind-pollinated species, in families with a greater diversity of growth forms, pollination mechanisms, and species distributions, in families at lower latitudes, in clades with hermaphroditic versus unisexual flowers, in plants with bilateral versus radial symmetry of flowers, in plants with hummingbird pollination

or with spurred or tubular flowers, in epiphytic lineages, and in young lineages (see review by Givnish, 2010a, as well as Ricklefs and Renner, 1994, 2000; Whittall and Hodges, 2007; Magallón and Castillo, 2009; Smith and Beaulieu, 2009; Givnish *et al.*, 2014). High rates of species diversification in the grass family (Poaceae) are correlated with the evolution of C_4 photosynthesis and climatic aridification in the Miocene (Spriggs *et al.*, 2014). High rates of diversification in orchids, the largest angiosperm family, are correlated with the evolution of pollinia, epiphytism, CAM photosynthesis, pollination by butterflies, moths, and euglossine bees, and (especially) life in extensive tropical cordilleras (Givnish *et al.*, 2015). As predicted long ago by Ehrlich and Raven (1964), speciation in mustards (order Brassicales) appears to have increased as a result of a coevolutionary arms race involving their chemical defenses and the detoxification abilities of the cabbage butterflies (family Pieridae) whose larvae feed on them. Edger *et al.* (2015) showed that species diversification in the

mustards accelerated with their evolution in sequence of indolic glucosinolates (mustard oils), then methionine-derived glucosinolates, then novel glucosinolate variants. Species diversification in pierids similarly accelerated with evolution of abilities to detoxify indolic, then methionine-derived, then structurally novel glucosinolates. Gene and genomic duplication events appear to have been involved on both sides of this arms race each time it escalated.

Evolutionary Convergence, Divergence, and Diversification within Plant Communities

Arid environments – Deserts are extreme environments, with very low mean rainfall ($< 25 \text{ cm y}^{-1}$), high to very high temperatures and low humidity in summer, cool to cold temperatures at night and during winter, and often thin, sandy or rocky soils. The great deserts of the world are mostly centered at 30° N and 30° S latitude, where large masses of hot, dry air descend to the surface after having ascended and lost their moisture via convective thunderstorms near the equator (Allaby, 2006). Dry conditions are exacerbated by the rain shadows created by mountains upwind, and by cold water offshore the western edge of continents. Rainfall is infrequent and highly variable from year to year, especially in deserts receiving the lowest mean rainfall. Where cold water is offshore and upwind (e.g., in the Colorado Desert of California), almost no rainfall falls in winter; when warmer water is offshore (e.g., in the Sonoran Desert of Mexico and Arizona), monsoons can also bring heavier rainfall during the summer months.

Convergence and divergence are both hallmarks of desert floras (Orians and Solbrig, 1977a). Desert plants include *drought avoiders*, *drought evaders*, and *drought tolerators*. *Drought*

avoiders include desert annual herbs that germinate after rains, and grow, flower, and set seed while the soil is relatively moist. In most deserts, these annuals are active almost exclusively after winter rainfall. In deserts with summer and winter rains, there are different groups of species that are summer and winter annuals. Annuals are short in stature, and allocate heavily to flowering and seed production. Species vary substantially in leaf thickness, reflectance, stomatal conductance, and photosynthetic capacity, from thick, hairy, silvery leaves with low rates of photosynthesis and transpiration, to thin, dark green leaves with high rates of photosynthesis and transpiration. *Drought evaders* include deciduous shrubs and herbs in the open desert, which shed their leaves when faced with drought, as well as phreatophytic trees, shrubs, and perennial herbs that live along washes and can tap a constant source of water. Washes serve as watercourses after rains, and substantial amounts of water brought by surface flow infiltrate their soils. Phreatophytes can tap a relatively permanent water table that is often several meters below the surface. *Drought tolerators* include evergreen shrubs like creosote bush (*Larrea*) with small, thick, tough leaves, and leaf or stem succulents like *Agave* and *Opuntia* that have CAM photosynthesis; these groups can also tolerate prolonged and intense droughts while retaining live leaves (Figure 5).

Among these growth forms, there is an inverse relationship between maximum photosynthetic rate per unit leaf mass and ability to maintain high photosynthetic rates as soil water content and water potential drop (Orians and Solbrig, 1977a,b). Desert annuals have the highest maximum rates of photosynthesis, but those rates are achieved with high stomatal conductance and rates of transpirational water loss, and so their photosynthetic rates drop rapidly as soils dry. Evergreen shrubs and especially succulents have much lower maximum rates of photosynthesis, but can remain active with



Figure 5 Examples of plant growth forms characteristic of the Sonoran desert of North America: (a) Stem succulent (saguaro, organ pipe, and cholla cacti (*Carnegieia*, *Stenocereus*, *Opuntia*) are visible) and drought-deciduous shrub (brittlebush (*Encelia farinosa* of the daisy family, with conspicuous yellow flowers and silvery leaves); (b) evergreen shrub (creosote bush (*Larrea divaricata*, family Zygophyllaceae) with narrow, tough leaves); (c) stem succulent with photosynthetic bark and drought-deciduous leaves (ocotillo (*Fouquieria splendens*), family Fouquieriaceae); (d) leaf succulent (*Agave palmeri*); (e) winter annual (*Phacelia calthifolia*, phlox family); and (f) summer annual (*Pectis papposa*, daisy family). All succulents shown have CAM photosynthesis except ocotillo, which is C_3 .

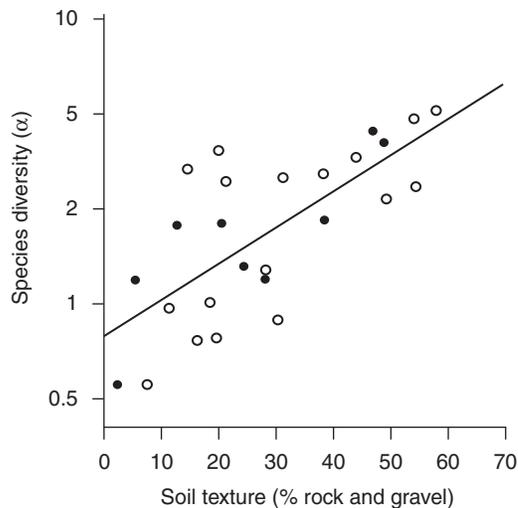


Figure 6 Species diversity (Fisher's α index) vs. soil texture in North American (\circ) and South American (\bullet) deserts (redrawn from [Orians and Solbrig, 1977a,b](#)). Note the convergence in the relationship of diversity to soil texture; more species are found per unit area on coarser soils with more rock and gravel.

relatively little fall-off in carbon capture even when soils are very dry (predawn water potential approximately -6 MPa). As a result of the inverse relationship between photosynthesis and its sensitivity to water potential, as soils dry after the winter (or summer) rains cease, there will be periods when each growth form – annuals, then deciduous herbs and shrubs, then evergreen shrubs, then succulents – has a photosynthetic advantage. The greater the range of moisture conditions present during a year, the greater the diversity of growth forms should thus be able to coexist, via a seasonal partitioning of photosynthetic advantage ([Orians and Solbrig, 1977b](#)). In deserts with sparse rainfall, coarse sandy or gravelly soils store the most moisture because they have high infiltration rates and little water is lost through evaporation at the surface after a storm; finer-grained soils have low infiltration rates and wind up storing less moisture. Consequently, we would expect the diversity of growth forms – and of plant species – to be higher on coarser soils. Indeed, [Orians and Solbrig \(1977b\)](#) found remarkably tight and similar relationships between species diversity and percentage of sand and gravel in deserts in Arizona and Argentina ([Figure 6](#)). Based on the alluvial sorting of soil texture, sites high on bajadas (desert slopes) have coarse soils and high diversities of both life forms and plant species, while those low on bajadas and alluvial flats have finer soils and lower diversities of life forms and species. In addition, in areas with lower rainfall – and thus, greater proportional variation in rainfall from year to year – deserts become increasingly dominated by annuals ([Schaffer and Gadgil, 1975](#)).

High rates of diversification are expected in desert annuals, based on their short life cycles ([Lewis, 1966](#)), tendency toward inbreeding ([Raven and Axelrod, 1978](#)), and dearth of effective means of long-distance seed dispersal ([Givnish, 2010a](#)). Little is known quantitatively on the actual rates of diversification, however. Over 2000 species of desert and vernal-pool annuals

comprise 26% of the vascular flora in the California Floristic Province, and most of these most likely arose in the last 15 million years following the uplift of the Sierra Nevada and the origin of winter rainfall ([Raven and Axelrod, 1978](#)). [Evans et al. \(2009\)](#) showed that a clade of *Oenothera* (Onagraceae, evening primrose family) composed almost exclusively of desert winter annuals spawned at least 11 species in 250 000 years, which would correspond to a net rate of species diversification $D (= \ln(S) T^{-1})$, where S is the number of species in a clade, and T is the stem age of that clade) of $9.6 \text{ sp sp}^{-1} \text{ My}^{-1}$ – an extraordinarily high rate that exceeds that of all plant groups studied to date (e.g., $D < 7.6 \text{ My}^{-1}$ for European *Dianthus* in the pink family ([Valente et al., 2010](#)); $D < 5.2 \text{ My}^{-1}$ for Andean *Lupinus* (lupine; [Drummond et al., 2012](#))). Succulents in the Aizoaceae (ice plant family) of the South African Karoo also have a high rate of species diversification ($D < 1.75 \text{ My}^{-1}$), but this appears related to their exceptionally poor powers of long-distance seed dispersal (splashed from capsules by raindrops) rather than their growth form ([Klak et al., 2004](#); [Ellis et al., 2006](#)).

Another mechanism that might promote high rates of diversification in desert winter annuals, and maintain high levels of species richness, involves competition across years based on their differential responses of germination, survival, growth, and seed production in response to variation in rainfall within a growing season ([Angert et al., 2009](#)). Annuals vary greatly in leaf thickness, reflectance, stomatal conductance, and photosynthetic capacity. Those with thin, green leaves have high photosynthetic rates and can produce large numbers of seeds in a rainy year, but are sensitive to drought; those with thicker, more silvery leaves have lower rates of photosynthesis and seed production but can survive in years with less rainfall. [Angert et al. \(2009\)](#) demonstrate that this tradeoff, combined with the high incidence of multi-year dormancy in winter annuals and their persistence in the seed bank, can permit a large diversity of annuals to coexist locally over long periods of time.

Across life forms, thicker, more reflective, and more steeply inclined leaves and lower stomatal conductance reduce water loss per unit leaf mass while reducing photosynthesis to a lesser extent. The high cost of water loss in dry environments, in terms of roots required to replace transpirational water losses, thus favors the evolution of thick, reflective leaves with low stomatal conductance. Narrow leaves reduce water loss per unit leaf area and increase convective cooling, and thus should also be favored in deserts ([Givnish, 1986](#)). Seasonal water shortage prevents perennial herbs or shrubs from covering the entire ground surface, allowing annuals – which perforce are short over much of their life cycle – to compete successfully with such taller plants. Low coverage, even after rains, favors short stature throughout the life cycle in desert annuals, and limited stature in perennial dominants ([Givnish, 1982](#); [Tilman, 1988](#)).

C_4 photosynthesis – while much less common than the C_3 photosynthetic pathway worldwide – often results in higher photosynthetic rates at low rates of transpirational water loss under warm, dry, sunny conditions. In deserts, C_4 photosynthesis is seen in many summer-active annuals and perennials, especially in grasses, sedges, amaranths, chenopods, and knotweeds, and is especially common in salt flats, where

reductions in water lost result in less energy being expended to excrete salt from the leaves, or to exclude it from being absorbed in the first place.

CAM photosynthesis reduces water loss even more than C_4 photosynthesis, although at the cost of greatly reduced carbon uptake. Not surprisingly, succulent plants with CAM photosynthesis are common in many deserts and semi-arid areas, including cacti and *Agave* species in New World deserts, and morphologically convergent *Aloe* and *Euphorbia* species in the Old World. Both C_4 and CAM involve CO_2 concentrating mechanisms that yield an advantage when atmospheric CO_2 levels are low. Cacti and *Agave* in the New World, and Aizoaceae in the Old World, underwent rapid species diversification starting 15 million years ago, suggesting that aridity and a drop in atmospheric CO_2 levels may have been drivers of a global diversification of succulent CAM plants (Arakaki *et al.*, 2011). A more detailed study, however, also suggests that the invasion of Central and North America as well as the rise of pollination by birds, bats, and hawkmoths may also have driven diversification in the cactus family (Hernández-Hernández *et al.*, 2014).

Among succulents generally, stature increases with the density of competing vegetation in which they occur: stone plants (*Lithops*, ice plant family) occur on nearly bare ground and are just a centimeter tall, while saguaro cacti – the tallest members of the cactus family – often grow in fairly dense desert woodlands on sites receiving abundant sheet flow, and can grow up to 12 m in height. Even so, desert succulents on different continents and in different families often show striking convergence, involving stem succulents in the cactus and spurge families (Cactaceae and Euphorbiaceae) in the New versus Old World, leaf succulents in the agave and aloe families (Agavaceae and Aloaceae) in the New World versus Africa, and bark succulents in the ocotillo and Madagascar succulent families (Fouquieriaceae and Didieraceae). Slow-growing but water-rich succulents defend themselves from herbivores with spines, stinging hairs, and caustic sap, and in some cases (e.g., the famous stone plants) may have avoided being eaten by ostriches through visual mimicry of the stony soil on which they grow. Some cacti (e.g., *Pediocactus* and *Sclerocactus*) have flattened, brown spines that appear to mimic the dried leaves of grasses among which they grow.

Alpine tundra – Alpine habitats above treeline on mountains are another kind of extreme environment, with low temperatures ($< 10^\circ C$ mean during summer), short growing seasons, frequent freeze–thaw cycles, cold winters, heavy UV irradiation, and in many localities, high winds, heavy snows, and thin soils (Körner, 2003). Treeline elevation varies from sea level at the continental limits to tree growth in the Arctic (ca. $60^\circ N$) and Antarctic (ca. $70^\circ S$) to 3800–4500 m in the tropics and subtropics. In areas with adequate moisture and soil, areas of continuous tree cover correspond roughly to areas with at least 100 days with mean temperatures $\geq 6.5^\circ C$ (Körner, 2003). The mean ground temperature at 46 treeline sites between $68^\circ N$ and $42^\circ S$ is $6.7^\circ \pm 0.8^\circ C$ (Körner and Paulsen, 2004). The strong correlation of treelines with thermal conditions strongly suggests that temperature is a key determinant of their position.

Although the limits of tree growth along moisture and light gradients has long been viewed to result from limited carbon

capture (Boysen-Jensen, 1949), some authors have stated that carbon limitation does not set the position of alpine treelines, despite the negative effects of lower temperatures and shorter growing seasons on carbon capture. Körner (1998, 2003) argued that the position of alpine treelines is set not by carbon limitation but by limitations of cell growth – especially of the roots – by cold temperatures. Trees roots should be especially vulnerable to this limitation because even short saplings would create cold soil conditions by shading the ground and insulating it with a thick layer of air; sunlit compact herbs and cushion shrubs should, on the other hand, warm the soil immediately below them well above air temperature. But the hypothetical limitation of root growth under tall plants would still leave carbon balance as a prime determinant of treeline position: taller plants would simply be unable to continue aboveground growth without matching root growth to enable absorption of water and nutrients, with negative effects on photosynthesis likely. In fact, tree height decreases smoothly and linearly with elevation in the European Alps, far below the range at which the hypothesized limitation of trees by cold soil would operate, with tree height at treeline of 5 m in Norway spruce (*Picea abies*) and 8 m in Swiss stone pine (*Pinus cembra*) (Paulsen *et al.*, 2000).

So an abrupt decline in maximum height by a few meters near treeline may, as argued by Körner, be driven by cold soils under taller trees and by an elevation of leaf temperature and hence photosynthesis by assuming a krummholz cushion form (Figure 7) within the ground boundary layer, but carbon limitation is important in setting treeline position. Recent CO_2 -addition experiments have confirmed an increase in growth by European larch (*Larix decidua*) but not Swiss mountain pine (*Pinus uncinata*) near treeline – clearly implicating carbon limitation – although the strength of this effect weakened after 6 years (Dawes *et al.*, 2015). Experimental warming of soils in the same experiment elevated growth by pine (but not larch), with the expected increase in root allocation.

In non-equatorial alpine environments, the dominant growth forms are krummholz, cushion shrubs, and compact to tall herbs (Körner, 2003). The aerodynamically smooth canopies of krummholz and cushion shrubs allow air to move past them without much mixing, permitting their leaves to warm $5\text{--}15^\circ C$ above the air only a meter or two above the ground boundary layer. Elevated leaf temperatures in a thermally limited environment can clearly be advantageous; such a benefit, as well as increased root temperatures, should also accrue to short herbs. In addition, smooth canopies of krummholz and cushion shrubs should divert winds around rather than through canopies, greatly reducing transpirational water loss under windy conditions, and decreasing sand- and ice-blasting of exposed plant parts. Desiccation or mechanical abrasion may indeed help shape the canopies of krummholz and cushion plants by eliminating projecting parts. Plants in many different families (e.g., Apiaceae, Asteraceae, Caryophyllaceae, Diapensiaceae, Ericaceae, Rubiaceae, Saxifragaceae, Stylidiaceae – the carrot, daisy, pink, diapensia, heath, coffee, saxifrage, and triggerplant families) have evolved this habit in alpine and arctic tundra communities across the Northern and Southern hemisphere. The warmth and sheltering influence of cushion plants, together with the moist



Figure 7 Krummholz of balsam fir (*Abies balsamea*) on Mt. Washington in northern New Hampshire.

soil they shelter, can permit them to have a beneficial effect on nearby plants in harsh alpine habitats (Badano and Lohengrin, 2006).

Narrow, thick leaves reduce water loss per unit leaf mass with small decreases to photosynthetic rate (see above), and so should be advantageous in alpine habitats with cold soils that restrict water uptake. Short-statured plants with streamlined canopies have advantages in elevating leaf temperature and reducing transpiration and mechanical damage in cold, windy alpine environments, but should be at a disadvantage in competing for light against taller competitors. Therefore, we expect taller competitors with looser canopies to replace short, cushion-form plants at lower elevations and in less exposed microsites, as can be frequently observed in many areas (e.g., see Billings and Mooney, 1968; Slack and Bell, 2014). Small changes in microtopographic position – involving shift of only a few centimeters – can have dramatic effects on wind exposure and snow accumulation, and on the plants inhabiting a microsite; such variation may partly account for the large numbers of species that co-occur in many alpine habitats. The short growing season in such habitats is, no doubt, responsible for their brief but spectacular period of flowering.

Frosts occur often throughout the growing season in many alpine environments, and increasingly so at higher elevations and more northerly exposures (Körner, 2003). Many species – including several cushion plants – have evolved the ability to supercool (that, chill below freezing without ice nucleation) or have internal ice barriers to prevent crystals from growing and damaging other parts of a plant once nucleation has begun (Kuprian *et al.*, 2014). Thermal gradients resulting from heating of the underlying soil by day can also prevent freezing damage to vegetative parts in cushion plants (Hacker *et al.*, 2011). The inflorescences of some plants project above the vegetative body and are therefore more exposed to both radiative and convective cooling, and somewhat decoupled from thermal inputs from the underlying soil. Reproductive shoots are often less frost resistant than vegetative shoots (which frequently can tolerate ice formation), but some species can supercool to at least $-22\text{ }^{\circ}\text{C}$ without damage (Kuprian *et al.*, 2014).

Frequent freeze–thaw cycles during the growing season can heave seedlings and small plants from the soil. This should

strongly favor plants which spread vegetatively and that do not depend as strongly on seedling establishment. Not surprisingly, 87% of vascular plant species in the Swiss alpine zone exhibit vegetative spread (Hartmann, 1957). Freeze–thaw cycles should hit seedlings of trees especially hard, given that they are non-clonal and have no vegetative connection to deep-rooted individuals.

Above treeline on equatorial mountains, there is essentially no thermal seasonality, but summer every day and winter every night (Hedberg, 1964; Smith and Young, 1987). Such communities are dominated by unbranched, giant rosette shrubs with marcescent leaves (i.e., those that persist on the stem after they die) (Figure 8). This highly unusual growth form has evolved convergently in *Espeletia* (daisy family) and *Puya* (bromeliad family) in Andean paramo and puna; in *Dendrosenecio* (daisy family) and *Lobelia* (lobelia family) in the Afro-alpine zone; and in *Agyroxiphium* (daisy family) and *Lobelia* in Hawaii. Different lineages evolved the giant rosette habit on different continents within the daisy and lobelia families (Knox, 2014; Givnish, 2010b).

The unbranched habit in equatorial alpine rosette shrubs permits concentration of foliage around a single terminal bud; in many species of *Espeletia* and *Dendrosenecio*, the heavily pubescent leaves wrap around the bud at night and prevent it from freezing and dying (Meinzer and Goldstein, 1986). In *Lobelia keniensis* of the wet Rwenzori Mountains in equatorial East Africa, rainwater collects among the tightly packed terminal leaf rosettes; its terminal buds apparently survive nightly frosts by sitting at the bottom of a small pool formed by the plant itself (Hedberg, 1964). The unbranched habit should also increase the rate of height growth, taking plants from the thermal extremes (frost by night, warm conditions by day) near the ground surface to more buffered conditions a meter or two above the ground (Smith and Young, 1987). The massive stems of the rosette shrubs enclose a large volume of pith; plants withdraw water from the pith early in the morning, when photosynthesis becomes possible after the sun rises but the plants are unable to withdraw water from the still-frozen ground (Meinzer and Goldstein, 1986). Species of *Espeletia* at higher elevations have a higher ratio of pith volume to leaf area, based either on a reversed elevational cline in plant height, or an increase in pith diameter. Leaf marcescence

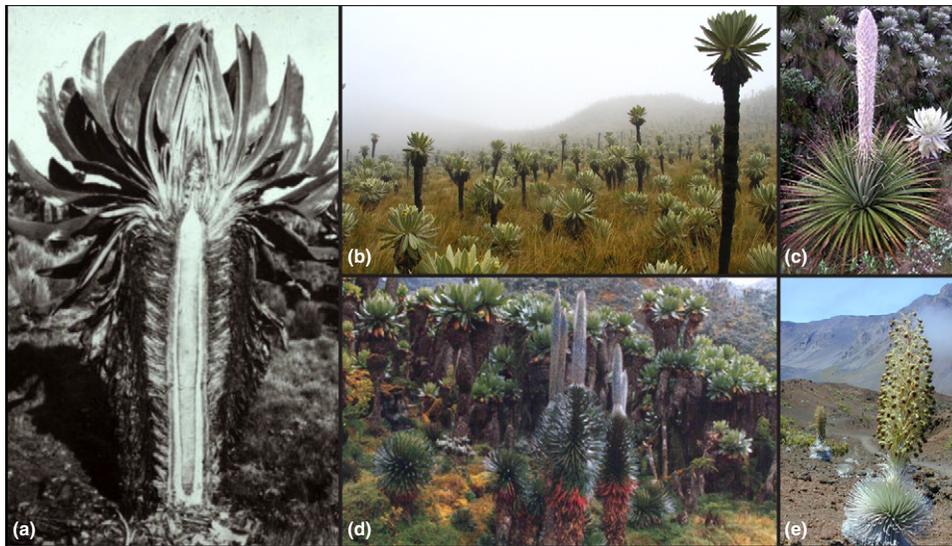


Figure 8 Giant rosette shrubs of the equatorial alpine zone. (a) Section through a *Dendrosenecio* (Asteraceae (daisy family)) from the equatorial alpine zone in East Africa; (b) stand of *Espeletia pycnophylla* in an Ecuadorean paramo; (c) *Puya clava-herculis* in an Ecuadorean paramo; (d) *Lobelia wollastonii* (with elongate, silvery inflorescences) and *Dendrosenecio adnivalis* growing in the Afro-alpine; and (e) Haleakela silversword (*Agryxophium sandwichense*, daisy family) growing near 3000 m elevation on east Maui.

produces an insulating blanket around the stem that prevents the pith from freezing and dying, and facilitates morning photosynthesis (Meinzer and Goldstein, 1986).

Alpine plants have undergone high rates of diversification around the globe, with rates D from 0.37 to 0.81 My^{-1} in Himalayan larkspurs (*Delphinium* subg. *Delphiniastrum*), 0.35 to 2.19 My^{-1} in New Zealand rock-cresses (*Pachycladon*), and 0.60 to 1.60 My^{-1} in Andean groundsels (Espelittiinae), 1.48 to 3.21 My^{-1} in Andean gentians (*Gentianella*), and 1.56 to 5.21 My^{-1} in Andean lupines (*Lupinus*) (Hughes and Atchison, 2015). Doubtless these high rates reflect the recent formation of many alpine regions through glacial retreat and orogeny, the archipelago-like nature of many mountain ranges, and the short life cycles of some of the plants involved.

Summary

Alpine habitats and deserts exemplify extreme environments, where plant growth and survival are strongly limited by one or a few factors, and where strong similarities in plant form or physiology often arise through convergent evolution and through species sorting along environmental gradients based on the traits with which different plants are endowed. Phenotypic divergence among species – reflecting divergent evolution, or species sorting based on dissimilarities among species – arises via competition. Closely related species are often very similar phenotypically and thus are each other's most intense competitors. Selection for divergence among species in habitat, form, physiology, or mutualists within a lineage leads to adaptive radiation; species sorting can lead to community assembly based partly on advantages accruing to species with similar traits adapted to environmental conditions, and based partly on advantages accruing to species with divergent traits that reduce competition among them. Under certain circumstances, adaptive radiation can lead to

accelerated rates of speciation and net species diversification. But limited dispersal, and differences among lineages in growth form, generation length, and extrinsic barriers to dispersal and gene flow within the habitats they occupy, may be as or more important in driving different rates of net species diversification.

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See also: C₄ and CAM Photosynthesis in Land Plants, Evolution and Diversification of. Parallel and Convergent Molecular Evolution

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