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SKY ISLANDS

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Sky islands are high-elevation habitats that are geographically subdivided and isolated among different mountain ranges (Fig. 1). Because of differences in climatic history and dispersal dynamics, the ecological and evolutionary processes and patterns characterizing sky islands may not always parallel those for traditional oceanic archipelago systems. Nevertheless, like their oceanic counterparts, sky islands are generators of diversity over multiple spatial and temporal scales and offer considerable potential

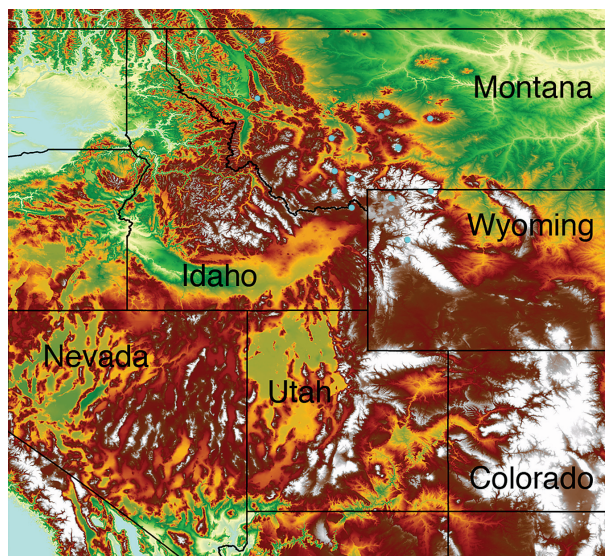


FIGURE 1 Map of the sky islands from the Rocky Mountains of northwestern North America. The distribution of the most likely habitat for montane grasshoppers in the genus *Melanoplus* is shown in white, as determined by ecological niche-modeling based on sampled populations (blue circles).

for investigating how different evolutionary processes such as natural selection and genetic drift lead to species formation.

BIOGEOGRAPHY OF SKY ISLANDS

The term “sky islands” was originally coined by Weldon Heald in his writings on the mountains of southeastern Arizona, which harbor isolated montane forest or woodland surrounded by a sea of desert (Fig. 2). Analogous to the water of oceanic archipelagoes, low-elevation habitat acts as a barrier to dispersal on sky islands, facilitating divergence of isolated populations. The general concept of sky islands has been expanded to include a variety of settings in which high-elevation habitats are separated by inhospitable lowlands, such as plateaus, ridges, páramos, and alpine meadows.

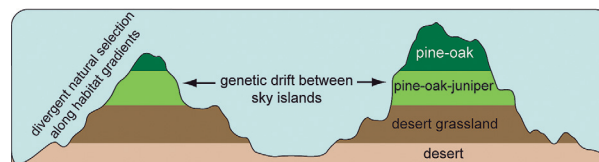


FIGURE 2 Schematic of the altitudinal distribution of habitats and examples of the evolutionary forces acting within and between typical Madrean sky islands of the southwestern United States and northern Mexico.

There are roughly 20 sky island complexes in the world (Table 1), each with a distinct origin, spatial arrangement, age, and climate history. As with oceanic archipelagoes, the geologic processes forming sky islands, which include volcanic activity, erosion, and mountain uplift, provide a temporal reference for determining the age of the islands. These differences have important consequences for evolution in sky islands. For example, ancient sky islands, such as those in the Pantepui region of Brazil, Guyana, and Venezuela, might be expected to show higher levels of divergence and species diversity than would younger sky islands. The Pantepui region formed through erosion of a formerly more widespread plateau that covered a large portion of the Guiana Shield. Rivers gouge this plateau, creating isolated, high-elevation mesas (tepui), which harbor cool, humid subtropical forests among the surrounding tropical lowlands. Many of the endemic species and subspecies found in this region are thought to have evolved in situ (i.e., they are not immigrants from non-sky island habitats) through isolation among tepuis. Similarly, the sky islands of the Cameroon Line in western Africa, which harbor many endemic species, were uplifted from lowland tropical forest during the Cretaceous

TABLE I
Sky Island Complexes Discussed in the Text

Name	Region	Description
Madrean archipelago	Southwestern United States (Arizona, New Mexico, and western Texas); Northern Mexico (Sonora, Chihuahua, and Coahuila)	Complex of 30–40 forested mountain ranges in the desert lowlands between the Rocky Mountains and Mexican Sierra Madres
Great Basin archipelago	Southwestern United States (Nevada and Western Utah)	Complex of ~200 mountain ranges arranged in close proximity surrounded by Great Basin desert
Rocky Mountains	Western United States (Colorado, Wyoming, Idaho, and Montana); Western Canada (British Columbia and Alberta)	Hundreds of isolated high-elevation meadows within a matrix of lower-elevation boreal forest
Ethiopian Highlands	Northeastern Africa (Ethiopia and Western Eritrea)	Mountain massif sundered by a rift valley with satellite forested mountains isolated by lowland desert and savanna
East African Arc	Eastern Africa (mainly Tanzania)	Circular complex of ~20 mountains (some of volcanic origin) harboring rain forest surrounded by arid woodland
Cameroon Line	Western Africa (Cameroon)	Linear chain of ~10 mountain ranges of volcanic and tectonic origin that also includes oceanic islands in the Gulf of Guinea
Annamite Range	Southeastern Asia (Vietnam and Laos)	Large cordillera and nearby satellite ranges of tropical rain forest and higher-elevation evergreen forest
Western Ghats	Southern India	Extremely isolated chain of ~5 mountain peaks harboring humid rain forest surrounded by arid lowlands
Pantepui region	Venezuela, Guyana, and northern Brazil	> 25 relictual plateaus of cool subtropical forest bisected by rivers and surrounded by tropical lowlands

NOTE: Many other sky island systems exist worldwide, as do other fragmented high-elevation habitats with characteristics similar to those of sky islands.

through tectonic and volcanic activity, and their large diversity of endemic species have apparently accumulated over this long history by in-situ speciation. Interestingly, oceanic islands in the nearby Gulf of Guinea formed concurrently through the same processes. The mountain isolates of the East African Arc, the Western Ghats in India, and the Annamite Range of Vietnam and Laos are also relatively old sky islands where differentiation among sky islands has promoted diversification. In contrast, the sky islands of North America, especially those in the Rocky Mountains, are relatively young geologically, on the order of 40–70 million years. Despite their short history, they have still promoted species diversification and have accumulated an impressive level of diversity.

Species in many sky island complexes, especially those in temperate regions, have experienced multiple and frequent climate-induced distributional shifts in association with the Pleistocene glacial cycles. This dynamic history contrasts with oceanic island systems, where inter-island dispersal is fairly rare and the geographic configuration of species across islands remains relatively constant over geologic time. Glacial cycles occurred regularly throughout the Pleistocene and intensified in the last 700,000 years, causing dramatic latitudinal and elevational shifts in species' distributions. During past glacial periods, displacement of sky island habitats to lower elevation meant that formerly isolated populations came into contact. This retreat into refugia was then followed by recolonization of

the isolated mountaintops as climate warmed during relatively short interglacial periods. Tropical sky islands—for example those in the Cameroon Line and the Ethiopian highlands—were also affected by Pleistocene glacial cycles through global cooling, although the effect was likely moderate compared to that occurring at higher latitudes. A dynamic history of climate change could potentially explain why the sky islands of the relatively high-latitude Madrean archipelago in the southwestern United States and northern Mexico have low levels of endemism despite harboring high diversity by virtue of lying at a crossroads of several biogeographic regions. In contrast, the climate regime of the sky islands of the endemic-rich East African Arc is thought to have been quite stable throughout the Pleistocene, thanks to the ameliorating influence of Indian Ocean currents.

In contrast to oceanic islands, colonization of sky islands can also occur through niche shifts from neighboring low-elevation habitats or through short-distance migration, in addition to long-distance colonization from other sky islands. For this reason, the dynamics of species assemblage in sky islands differ in many ways from the equilibrium theory of island biogeography set forth by MacArthur and Wilson in 1967, which postulates that island species diversity is a balance between colonization (distance between habitat patches) and extinction (size of patch). Research by Brown and colleagues showed that species composition of mountaintop mammals in the

Great Basin was largely governed by extinction and that the type of habitat that potential colonizers had to traverse to reach a new island, rather than geographic distance per se, determined when colonization by immigration was likely. Studies on birds were more consistent with predictions of the theory of island biogeography, showing an effect of habitat area and degree of isolation on species diversity and endemism. One particularly extreme example is the Sierra del Carmen of northern Coahuila, Mexico, an isolated sky island that shows strong effects of insularity typical of oceanic islands, including reduced species diversity and resulting ecological niche expansion, and augmented density of several resident bird species.

SKY ISLANDS: WINDOWS INTO EVOLUTIONARY PROCESS

Sky islands, like oceanic islands, are ideal settings for evolutionary study. The replicated spatial arrangement of similar, isolated habitats provides a natural experiment for determining what ecological and geographic features facilitate diversification. Selection and genetic drift are both particularly powerful in island systems: The isolation between islands is conducive to divergence by genetic drift, whereas opportunities for selection may occur because of differences in ecology or factors relevant to sexual selection among islands.

Additionally, divergence by natural selection might occur across altitudinal gradients within individual sky islands. For example, the Madrean sky islands are distributed among 30–40 mountain ranges of various sizes and orientations that link the Sierra Madre massifs with the Rocky Mountains in stepping-stone fashion. The present configuration of habitats within these sky islands is post-glacial (less than 20,000 years ago). Whereas relatively contiguous woodlands covered the region during glacial periods, there is greater habitat contrast in the Madrean sky islands today: arid oak woodlands in low-elevation canyon, mid-elevation pine-oak forest, and boreal forest in some of the highest-elevation sky islands (Fig. 3). These ecological transitions are comparable to changes manifest at much larger geographic distances (e.g., over hundreds of kilometers in latitude), yet in sky islands they occur over just a few kilometers—and within the dispersal capacity of most species. Plant and animal populations that span these ecological transitions experience drastically different environments, both abiotic (e.g., rainfall and temperature) and biotic (e.g., food resources, competitors, and predators), which can result in divergent selective pressures. If strong enough, selection can generate observable differences between populations that are connected by



FIGURE 3 The Chisos Mountains, a sky island in Big Bend National Park in southwestern Texas and part of the Madrean archipelago. Chihuahuan desert gives way to desert grassland at mid-elevation and pine forest at high elevation. The nearest sky island is the Sierra del Carmen in northern Coahuila, Mexico, approximately 60 km away.

gene flow. This “gradient model” of divergence has been validated by empirical studies showing elevational diversification of ecologically divergent sibling species as well as population-level divergence in adaptive morphology.

SKY ISLANDS AS GENERATORS OF DIVERSITY

Much debate surrounds how species diversification has been promoted in sky islands. The likely effect of isolation among sky islands on the formation of new species is not controversial; however, the effect of the Pleistocene glacial cycles on species divergence is a contentious issue. Because of the relatively short amount of time between glacial cycles, there are disagreements over whether diversification would have been inhibited or promoted. Although divergence is expected within sky islands from the divergent selective pressures generated from altitudinal habitat differences, as well as from opportunities for differentiation among isolated sky islands by genetic drift and/or selection, differentiation among populations that accumulated during one glacial cycle may have been lost during subsequent distributional shifts. Alternatively, if sufficient reproductive isolation evolved in any one cycle, speciation could actually have been promoted by the frequent distributional shifts, as hypothesized by the “species pump” model of diversification.

Molecular data play a critical role in distinguishing among evolutionary scenarios, as neutral genetic markers provide a means for estimating the timing of divergence and reconstructing the history of divergence across the sky island landscape. In the Madrean archipelago, fossilized plant material from packrat (*Neotoma* spp.) nests has allowed for a thorough reconstruction of paleohabitats through the last glacial maximum. According to these

data, fragmentation of sky islands occurred approximately 10,000 years ago, offering a hypothesis that can be tested with intraspecific genetic data from sky island species. So far, molecular studies in this region have produced conflicting results on the timing of divergence, with some species showing no evidence for postglacial divergence among sky islands and other species showing evidence for divergence much older than the last glaciation. This discord between paleoecological and genetic data can be attributed in part to the difficulty of detecting and timing recent genetic divergence. Large sample sizes and thorough regional sampling will undoubtedly be necessary to thoroughly test this hypothesis.

What has emerged from the many molecular phylogenetic and phylogeographic studies on sky islands is that some species show strong patterns of differentiation that are coincident with the glacial cycles, whereas divergence predates the Pleistocene in other taxa. For example, in the northern Rocky Mountains of North America, some insect groups, such as flightless montane grasshoppers in the genus *Melanoplus*, radiated during the Pleistocene. Genetic data indicate that divergence among multiple glacial refugia, as well as differentiation during the recolonization of sky islands, was facilitated by genetic drift. However, sexual selection has also been implicated in this diversification because of the rapid divergence in male genitalia, which can play a role in reproductive isolation. Sexual selection has also likely been important to incipient speciation among populations of a jumping spider (*Habronattus pugillis*) in the Madrean archipelago. Populations on different mountains have divergent phenotypes, seismic songs, and courtship displays, which result in mating incompatibilities between forms. Also in the Madrean archipelago, pollinator-mediated natural selection seems to be influencing morphological differentiation among populations of a perennial plant (*Macromeria viridiflora*). Thus, in North American sky island systems, natural selection, sexual selection, and genetic drift all appear to be important evolutionary processes driving Pleistocene diversification. However, the timing of speciation in other taxa from the Rocky Mountains—most notably the mammals—predates the Pleistocene, suggesting that divergence in these species may have been inhibited by the frequent displacements from their sky island habitats.

A pattern of pre-Pleistocene origination also has been found in a number of tropical bird and mammal species, casting doubt on the hypothesized “species pump” model of diversification among tropical sky islands. Nevertheless, diversification of tropical taxa across sky islands, albeit

pre-Pleistocene, demonstrates how this geographic setting is conducive to divergence. More examples of divergence among sky islands in tropical regions will undoubtedly be uncovered with further study and will be important for confirming that tropical sky islands do not conform to the “species pump” model of diversification.

Regardless of the timing of diversification, sky islands are clearly promoters of diversification from the level of the population to the species. Despite the fact that our most thorough descriptions of genetic and phenotypic divergence in sky islands come from temperate North America, this sampling bias should not be taken as evidence that tropical sky islands are not important centers of diversification. In the Pantepui region of South America, for example, passerine birds (genus *Myioborus* and *Atlapetes*) have differentiated at both the subspecies and species level among the isolated plateaus. Similarly, populations of poison dart frogs inhabiting sky peninsulas in central Peru have diverged rapidly in coloration despite close proximity. In a particularly thorough study of the starred robin (*Pogonocichla stellata*) on sky islands in the East African Arc, Rauri Bowie and colleagues showed how considerable genetic diversification has accumulated among phenotypically divergent sky island populations. Further studies promise to reveal more about patterns and timing of diversification in tropical sky islands, which have been little explored compared to their temperate counterparts. Lastly, such information will also provide an interesting counterpart to the considerable attention given to the diversification across isolated tropical habitat fragments, such as the remnants of previously widespread wet-tropical forest fragments found in North Queensland, Australia.

IMPACT OF HUMAN-INDUCED CLIMATE CHANGE ON SKY ISLANDS

Climate change poses a unique threat to sky islands. Temperature increases of as little as a few degrees could push sky island habitats to higher elevations, reducing their area and potentially causing local extinction of endemic taxa and divergent populations harboring unique genetic and phenotypic diversity. Sky islands in North America and Mexico are already being affected by climate change, with increases in drought, fire, and outbreaks of invasive insects. Although these resilient systems have endured large-scale shifts in climate throughout the Pleistocene, the pace of human-induced climate change may represent an insurmountable challenge for sky islands, with potentially devastating consequences to their biodiversity and evolutionary potential.

SEE ALSO THE FOLLOWING ARTICLES

Fragmentation / Island Biogeography, Theory of / Pantepui /
Refugia / Sexual Selection

FURTHER READING

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SNAILS

SEE LAND SNAILS

SNAKES

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Snakes (3000+ spp.) are a highly specialized and successful limbless form of lizard. Their low metabolic rate combined with jaw anatomy that accommodates the ingestion of relatively prodigious meals allows snakes the energetic option of long fasts between large meals, permitting them to rely on infrequent food sources such as annually nesting birds. Avian and mammalian predators require more continuous food sources and therefore cannot survive on islands lacking year-round prey. Accordingly, snakes are the top predator on many islands, especially land-bridge

islands that experience pulses of visiting birds. However, snakes are rare on most oceanic islands because they are not well suited for dispersing across saltwater. Snakes may dramatically rearrange the vertebrate ecology of formerly snake-free oceanic islands when they are introduced by humans.

EVOLUTION

Snakes were the last major group of reptiles to appear, evolving from a varanid lizard-like progenitor at least 135 million years ago. Because the eyes of snakes are radically different from those of their immediate lizard ancestors, proto-snakes are believed to have passed through an evolutionary transition in which their eyes degenerated as a result of living underground or in murky water. Returning to the aboveground environs suited them well and set off an adaptive radiation yielding over 3000 modern species, covering all habitats except high arctic and cold marine environments.

What are the ingredients for this evolutionary success? One is a superbly developed ability to smell prey, perhaps a benefit retained from the time spent underground or in murky water. Another is the loss of legs. Leglessness facilitates locomotion underground, in vegetative thickets, and in water. Another is their ectothermic heritage, which saved them the expense of having to feed continuously to generate heat. The low metabolic cost of ectothermy allows a predatory style that emphasizes stealth, patience, and surprise over speed and endurance. Mammals and birds are incessantly in motion, searching insatiably for each next bite of food; snakes are well suited to the complementary lifestyle: patiently conserving energy while waiting for a frenetic endotherm to wander within striking range. A less obvious asset of snakes is their very light and supple jaws, which arose in the course of ophidian evolution to permit the ingestion of extraordinarily large meals (at maximum, more than 100% of their body mass). These lightweight jaws are unsuited for biting prey into submission, so snakes developed constriction and venom (or perhaps their possession of venom and constriction enabled the concurrent evolution of lightweight jaws).

Thus, snakes are often successful by virtue of visual- and olfactory-targeted sit-and-wait predation from the security and concealment of water, a burrow, or a thicket. Sit-and-wait snakes generally subdue their prey by venom or constriction. Other snakes are successful by patrolling for relatively defenseless prey, such as eggs, that are large but rarely found: Having low metabolic needs, the snake can afford to wait for the rare but highly rewarding (i.e., large) prey item.