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**Rocky Mountain
Forest and Range
Experiment Station**

Fort Collins,
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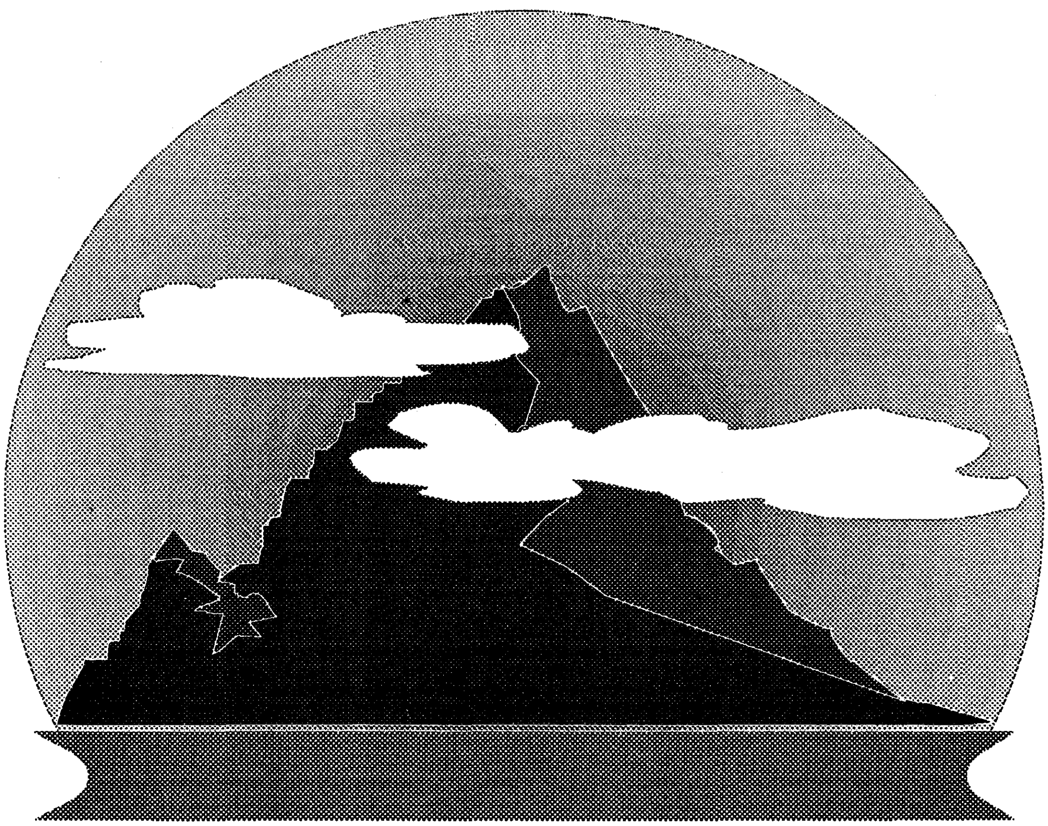
**General Technical
Report RM-GTR-264**

Biodiversity and Management of the Madrean Archipelago:

The Sky Islands of Southwestern United States and Northwestern Mexico

**September 19-23, 1994
Tucson, Arizona**



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The Madrean Sky Island Archipelago: A Planetary Overview

Peter Warshall[1]

Abstract.—Previous work on biogeographic isolation has concerned itself with oceanic island chains, islands associated with continents, fringing archipelagos, and bodies of water such as the African lake system which serve as "aquatic islands". This paper reviews the "continental islands" and compares them to the Madrean sky island archipelago. The geological, hydrological, and climatic context for the Afroalpine, Guyana, Paramo, low and high desert of the Great Basin, etc. archipelagos are compared for source areas, number of islands, isolating mechanisms, interactive ecosystems, and evolutionary history. The history of scientific exploration and fieldwork for the Madrean Archipelago and its unique status among the planet's archipelagos are summarized.

In 1957, Joe Marshall published "Birds of the Pine-Oak Woodland in Southern Arizona and Adjacent Mexico." Never surpassed, this elegant monograph described the stacking of biotic communities on each island mountain from the Mogollon Rim to the Sierra Madre. He defined the Madrean archipelago as those island mountains with a pine-oak woodland. In 1967, Weldon Heald (1993), from his home in the Chiricahuas, coined the addictive phrase—"sky islands" for these insular mountains of the North American borderlands. Weldon Heald's catch phrase immortalized Joe Marshall's meticulous observations. Today's conference is the first solely dedicated to understanding Madrean sky island biology, beauty, and needs for management and conservation.

There are about 40 sky islands (fig. 1) between the Mogollon Rim and the Sierra Madre Occidental (Warshall, in press). Mt. Graham on the Pinaleno mountains is the tallest peak (10,712 feet). Relief between valleys and peaks ranges from 1250 to 6750 feet (McLaughlin, 1992), but is typically between 3000 and 5000 feet. The Madrean region has exceptional species richness, super-species complexes, unusual neoendemics and archeoendemics, an exceptional mixture of species from the Nearctic and Neotropic regions, important influences from the eastern (North American Prairies Province of Takhtajan, 1986) and western biogeographic provinces, a wealth of genetically unique cultivars in the Sierra Madre Occidental, and a myriad of mysteries concerning the distribution of disjuncts, species "holes," and species "outliers" on individual mountains (e.g., Ramamoorthy, 1993). The northernmost sky islands are the only place in North America where you can climb from the desert to northern Canada in a matter of hours (Warshall, 1986). The sky islands pose numerous puzzles about vertical migration strategies used by plants and animals both annually and over glacial time periods.

These interests in ecology and evolution mix with the other citizen interests in skiing, grazing, hunting, fishing, escaping the heat, summer homes, telescopes and radio towers, bird watching, rock-climbing, military practice maneuvers, fuelwood cutting, camping, mining, sacred Native American values and ceremonies, archaeological sites, as well as preservation of sky island habitat for threatened and endangered species. Underpinning all these interests is the exceptional beauty of the sky islands—their layering of peaks in a dusty sunset, lines of vibrant riparian along arid yellow slopes, the contrast of snow and desert, the baffling complexity of erratic ridge lines, the power of fires, and the subtle tones of blue-gray limestone, speckled granite, and pastel volcanics.

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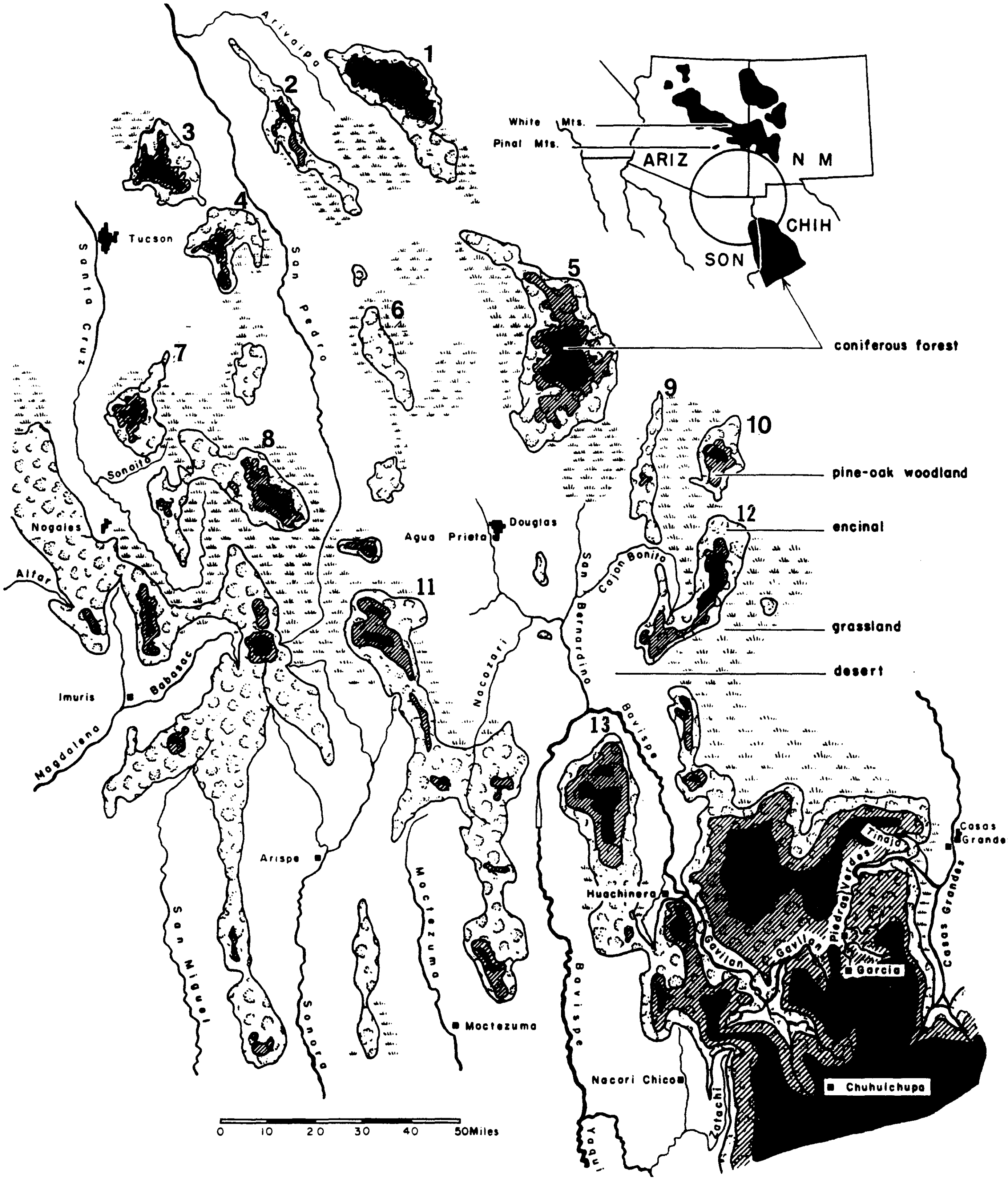

Figure 1.—The Madrean Sky Island archipelago (based on Marshall, 1957).

WHAT ARE SKY ISLANDS?

Sky islands are a type of continental or inland terrain made up of a sequence of valleys and mountains. All sky islands have a stack of biotic communities that allow vertical (as well as aspect) migration annually or during one of the planet's long-term climatic events. The valleys act as barriers or bridges to the colonization by new species that attempt to cross the intervening valley. The valleys become barriers when they contain an ecology alien to the migrating species. By analogy with the saltwater seas between oceanic islands, the higher elevation biotic communities of sky island mountains are isolated by each valley's "sea" of alien vegetation. The mountains, like the Galapagos or other oceanic islands, act as isolated cradles of evolution.

In the Madrean archipelago, the valleys and mountains are roughly parallel. The stacked biotic communities (fig. 2) include: montane coniferous forests; oak-pine (coniferous) woodlands; tropical deciduous forest; oak savanna (deciduous vs. evergreen oaks predominate); short-grass prairie; subtropical thornscrub; and subtropical desert (Brown, 1982). The "heart" of the Madrean archipelago (its defining characteristic) is the oak-pine woodlands (Marshall, 1957). The barrier "seas" include the short-grass prairie, the subtropical thornscrub, and subtropical desert.

SKY ISLANDS OF THE PLANET

There are about twenty sky island complexes on the planet (table 1 and fig. 3). All the continents with, perhaps, the exception of Australia, harbor sky island complexes. The information on the sky island complexes of Eurasia, China, and southeast Asia remains incomplete because of the difficulty of obtaining English translations (Suslov, 1961; Aiken, 1992). Most of the literature has focused on the mountains themselves, not the importance of the valleys between them. There has been remarkably lithe work comparing the planet's continental island ecosystems (Carlquist, 1963), their palaeogeographic history, floristic and faunal source areas, and valley barriers.

By creating a parallel typology with recent classifications of oceanic islands such as isolated island "chains" (Hawaii), "continent associates" (Madagascar, Philippines), and "fringing archipelagos" (the southern Japanese or Sea of Cortez island groups), we can approximate a classification for the continental islands. Table 1 classifies continental island clusters on the basis of their geographic axis, latitude, whether they are coastal or inland, the number per complex, and the configuration of each grouping. Configurations include: stepping stone archipelagos (mountains and valleys spaced between two cordilleras), isolated massif(s) with outlier sky islands, linear

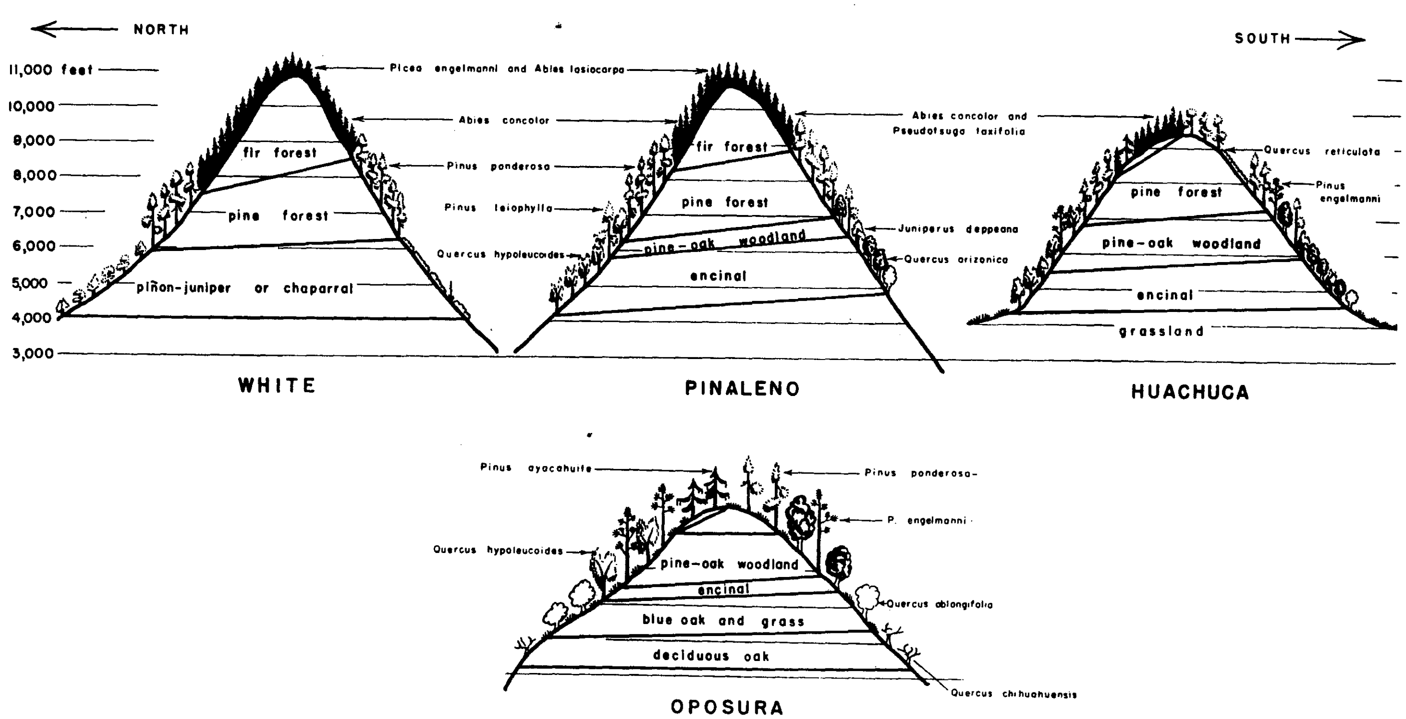

Figure 2.—Example "stacking" of biotic communities of the Madrean archipelago (Marshall, 1957). Note the position of the oak-pine woodlands.

chains of outlier mountains/valleys at one end of a cordillera, and completely isolated groups of mountains. A surprisingly large number of complexes (e.g., the Adamoua, Baja Peninsula, and East African arc) contain both oceanic islands and sky islands with both saltwater and vegetative "seas." Like all typologies, there are ambiguously categorized groupings.

Planetary Examples

The four descriptive variables used to classify sky islands act in concert. Compare the Madrean stepping stone configuration with the isolated archipelago of the Western Ghats of India (not illustrated), the isolated cluster of the Pantepuis of Brazil, Guyana, and Venezuela (fig. 5) and the East African arc and the Ethiopian massif complexes (fig. 6) . The Western Ghats (Manickam, 1992) comprise a north-south cluster of tropical mountains spanning about six degrees of latitude.

Table 1.—Sky Island Types

Type	Examples
Stepping stone archipelago between two mountain chains	Madrean archipelago Great Basin archipelago Altai/Tien Shan Basin Meso-American massifs
Isolated massif with outliers	Ethiopian highlands East African arc Saharan massifs Atlas Mountains Jabal Lubnan Adoumoua Mountains Drakenbergs Central European massifs Caucaso-Iranian massifs
Cordillera with outliers	Chaine Annimatique (Vietnam) Malay peninsula Baja California peninsula Coastal Cordillera (SA) Southern Andes
Isolated sky island chains	Western Ghats Pantepuis
High altitude sky islands	Punas and paramos (SA) Himalayas

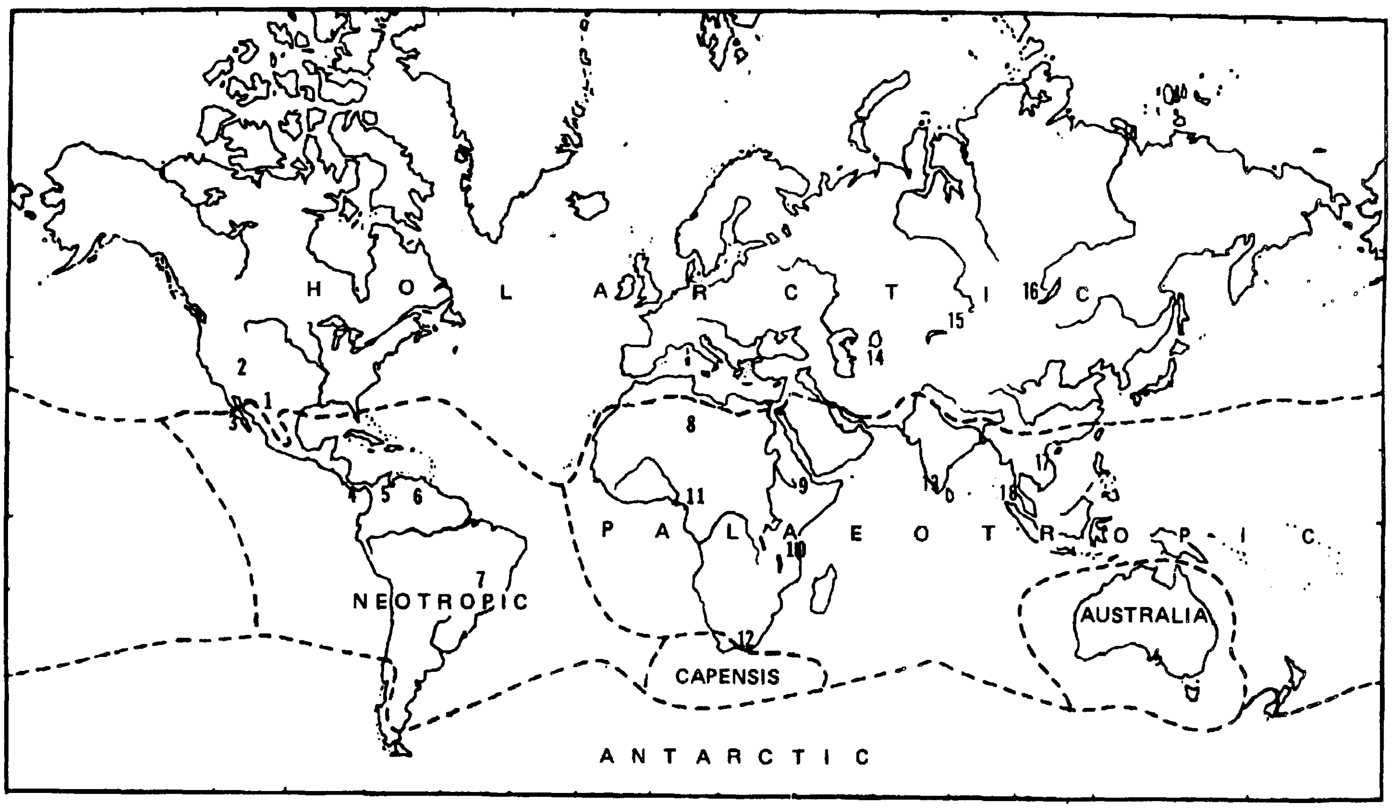

Figure 3.—Locations of sky island complexes mentioned in text on a map of the Floristic Realms of the planet. Only the Madrean archipelago straddles two; Floristic Realms. (1) Madrean; (2) Great Basin; (3) Baja California (4) Meso American; (5) Coastal Cordillera; (6) Pantepuis; (7) Brazilian shield; (8) Saharan massifs; (9) Ethiopian Highlands; (10) East African arc; (11) Cameroon Bight; (12) Southern African complex; (13) Western Ghats; (14) Caucaso Iranian massifs; (15) Altai/Tien Shan; (16) Trans-Baikal; (17) ChaineAnnimatique; (18) Malay peninsula. High valley "islands" can be found in the northern Andes and Himalayas.

They are isolated from the nearest cordillera, the Himalayas, by over 1,200 miles. The Western Ghats are further isolated to the south and west by the Laccadive Sea. On the north and east, the valley barriers are, at the present, highly humanized landscapes with pockets of Deccan thornforests. The Western Ghats contain about five distinct mountain with one major valley (the Palghat gap) subdividing the archipelago. Sometimes, Sri Lanka has been included as an oceanic island within the sky island archipelago. In part, the high endemism of the montane Malabar rainforests which cover the Western Ghats can be traced to its former Gondwanaland connection.

The Pantepuis (Minestero, 1985; Fittkau, 1969; Steyermark, 1982; deGranville, 1982; Haffer, 1987) form a scattered, isolated tropical series of 15 large and 20 smaller sky islands. The Pantepuis cluster shows no distinct axial direction and relief is relatively small (about 2000 feet). In this part of South America, a "tepui" means a "sky island." The major "barriers" isolating the individual tepuis are rivers, many with "blackwater" (acid) waters. The southern boundary, the gigantic Amazon Basin, separates it from the sky island complex of the Brazilian shield, over 1500 miles away. Both the Pantepuis and the shield once were parts of the same plateau and contain numerous parallel taxa. On the west, the Orinoco River and, to the east, the Essequibo River act as major barriers. Only to the northeast do a few tepuis approach the outlier mountains of the coastal cordillera, including the offshore islands along the Caribbean coast. The inter-mountain valley "seas" include savanna, caatinga, and chaparral as well as the "blackwater" rivers.

Both the Ethiopian complex and the Zanj or East African arc complex (Kingdon, 1990) gained their relief from the great East African rift valley (see below). The Ethiopian complex centers on the high elevation basaltic plateau that rifted into two massifs (the Simien and Bali mountains). The Ethiopian complex is isolated by the White Nile to the west; the Kenyan, Somalian and Saudi deserts as well as the Red and Arabian Seas. It has a strong north-south axis covering seventeen degrees of latitude with fifteen to twenty peaks greater than 9,000 feet in elevation. The relief is typically 5000 feet. The valley barriers include harsh desert, acacia/commiphora bushland, and dry savanna. The isolated biotic communities include the higher elevation juniper / podocarpus, montane bamboo, ericaceous tree / shrub and afro-alpine belts. In its largest dimensions, the Ethiopian sky island complex includes the

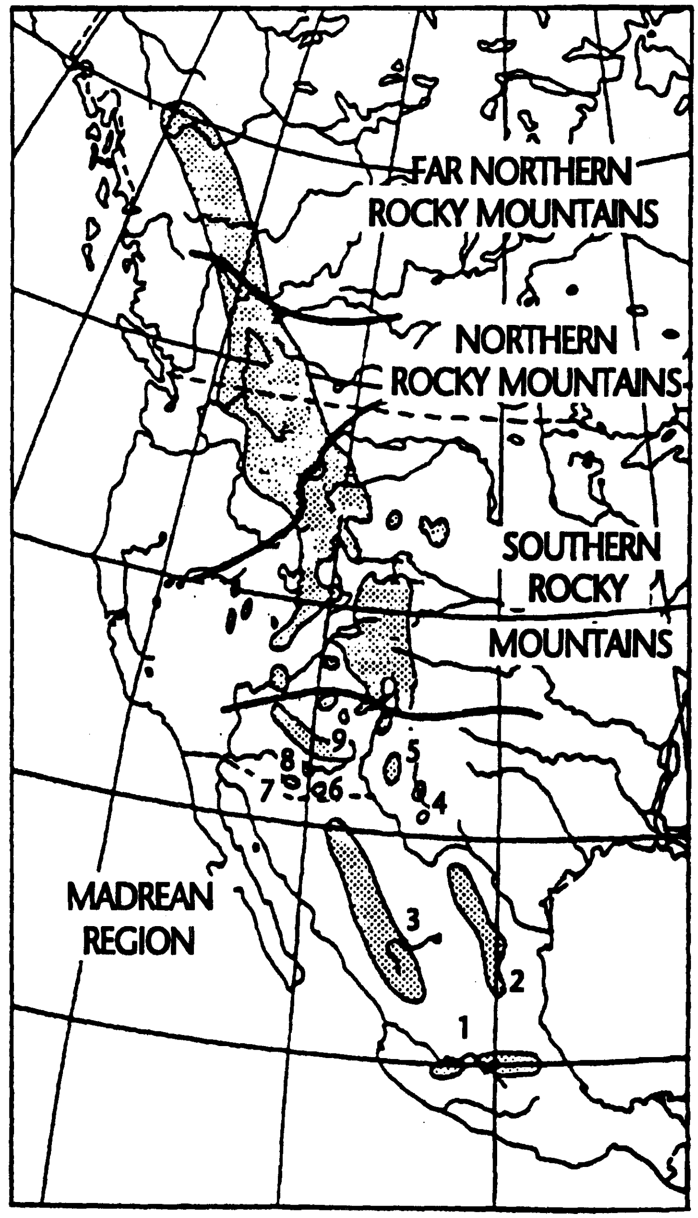

Figure 4.—Location of the archipelago as a stepping stone between the Rocky Mountain cordillera to the north and the Sierra Madre to the south (modified from Peet, 1988). Approximate boundaries of the four major floristic provinces indicated by solid lines. Major Sierra Madre mountains include: (1) Trans-Mexican volcanic belt; (2) Sierra Madre Oriental, and (3) the Sierra Madre Occidental which is the nearest Mexican source area for the Madrean archipelago.

The Madrean sky islands shown include (6) Chiricahua mountains, (7) Santa Catalina Mountains, and the (8) Pinalenos Mountains. The Mogollon Mesa (9) is the nearest Rocky Mountain source area for the Madrean archipelago.

The Sierra Madre Oriental sky island complex includes (4) the Davis Mountains and (5) Sierra Blanca.

Asir/Hadramawt sky island complex of Yemen and Saudi Arabia.

The East African arc massifs, sky islands and three oceanic islands (Pemba, Mafia, and Zanzibar) create a rough geographic circle involv-

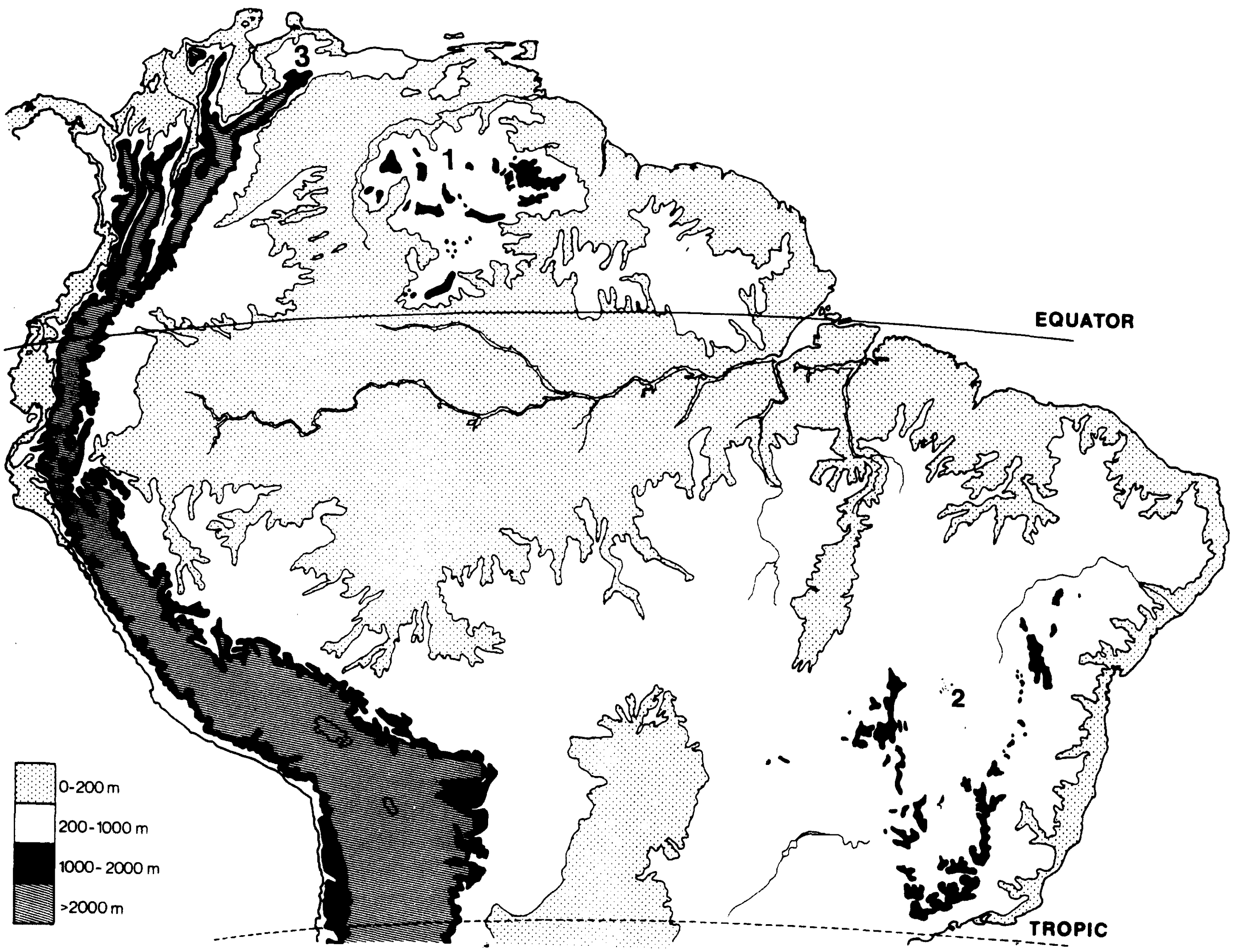

Figure 5.—Three South American sky island complexes are shown: (1) The pantepuis; (2) the Brazilian shield; and (3) the Coastal Cordillera.

ing seven African nations and twelve degrees of equatorial latitude (fig. 6). The circle comprises older massifs such as the Ruwenzori (Monts Mitumbe), Kipengere, and Udzungwa ranges; the Nyika and Rukiga plateaus, and the Mau escarpment combined with many more recent isolated mountains including the Usambara, Uluguru, Mt. Kilimanjaro, Mt. Meru, and Mt. Elgon. Relief exceeds 9,000 feet for the seven highest isolated volcanos. Rift valley lakes (e.g., Lake Victoria and Lake Tanganyika) and, of course, the Congo River Basin and Indian Ocean act as important barriers to gene flow. The valley barrier is predominantly savanna. The montane communities parallel those of the Ethiopian massif.

Finally, the north Andes and Himalayas contain a contrasting variant - high altitude island *valleys*.. These cordilleras have "sky island" valleys or plateaus embedded within the mountain ranges. The valleys contain exceptional pockets of endemism. For instance, the South American paramos (the alpine belt) have acted as "population traps" during repeated glacial events (Prance, 1987; Kant, 1989; Haffer, 1987). These high elevation, sky island valleys form a special group of continental islands similar to isolated lakes (e.g., Baikal, Malawi) and caves.

The Madrean Archipelago: Comparisons

The Madrean archipelago is a "stepping stone archipelago" between two mountain chains (the Rocky Mountains and its plateaus and the Sierra Madre plateau and its mountains) arranged in a roughly north-south axis (figs. 1 and 4). Archipelagos between two cordilleras may have greater opportunities to increase biological diversity because the configuration provides two source areas instead of one. In general, north-south axes (e.g., the Madrean archipelago, Baja Peninsula, Western Ghats, Malay Peninsula) also provide for a greater amount of climatic variation than east-west axes (e.g., the Himalayas, Eurasian ranges, Coastal Cordillera of South America) and, perhaps, greater potential for evolutionary differentiation. Compare the Madrean archipelago to the Great Basin. The Great Basin is a sky island cluster two cordilleras but its axis, between two major source areas, is predominantly east to west.

The Madrean archipelago is a mid-latitude sky island complex, along with the Saharan massifs, the South African complex, the Atlas Mountains (Morocco), the Great Basin, the Baja California peninsula, and perhaps a range in China. (Other possible mid-latitude sky islands complexes" the Caucaso-Iranian, Central European Highlands, Jabal Lubnan—appear to be so altered by human influences that it is difficult to determine what biological information remains.) These mid-latitude complexes experience greater annual and decadal climatic flux. The Madrean is unique, even among mid-latitude sky island complexes, because temperate and subtropical climatic regions interfinger with tropical climates found in the Caribbean.

The tropical sky island complexes include the Meso-American massifs; Ethiopian and Adamoua and East African highlands in Africa; the Coastal Cordillera, the Pantepuis and Brazilian Shield clusters of South America; and the Western Ghats, the Malay Peninsula and Chaine Annimatique of

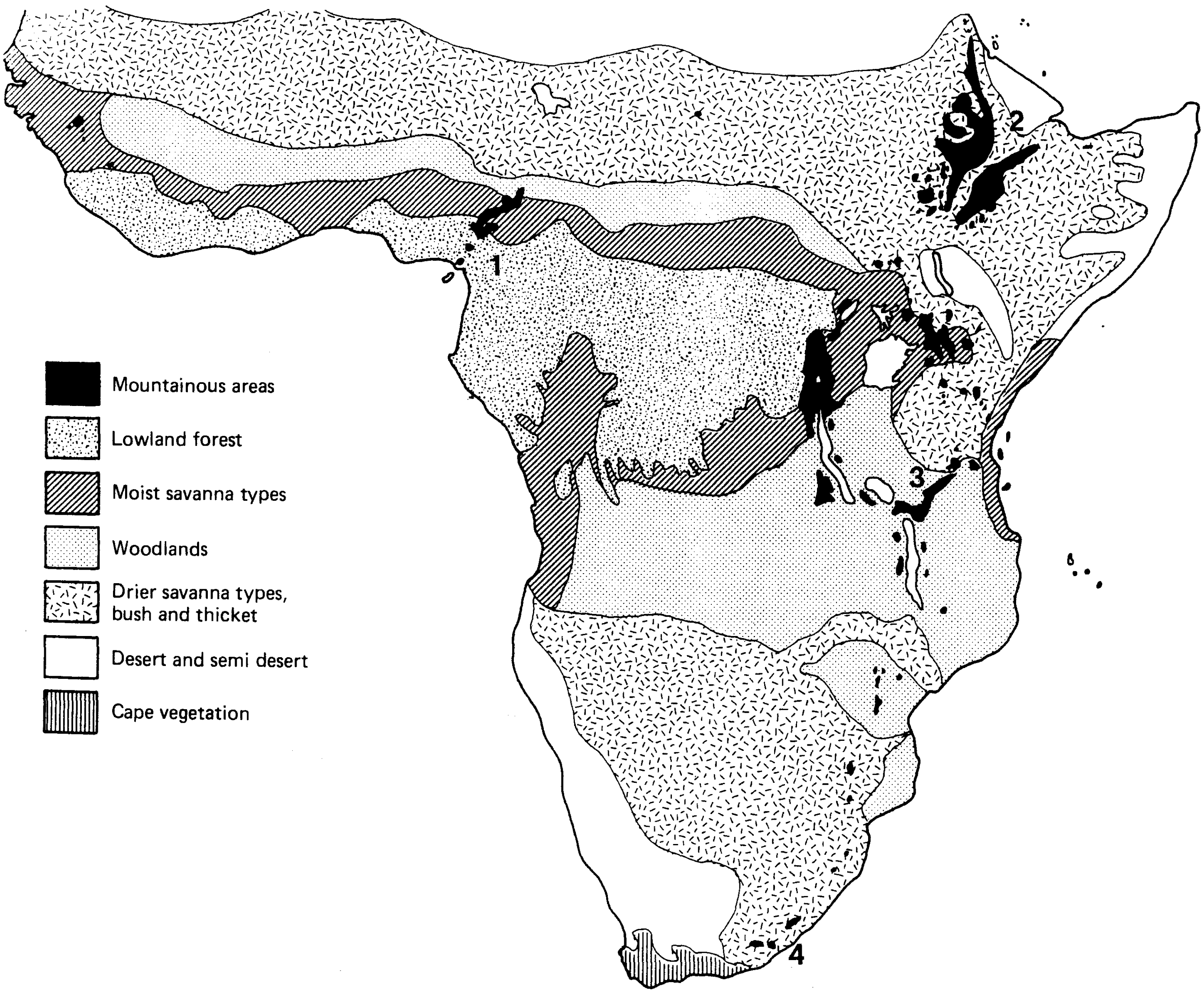

Figure 6.—Four African sky island complexes are shown: (1) The Adoumoua chain in Cameroons; (2) the Ethiopian Highland complex; (3) the East African arc complex or Zanj; and (4) the South African complex.

South Asia. In recent geological time, the fluctuation of pluvials or inter-pluvials has had a major influence on whether the valley vegetation was a bridge or a barrier. The Ethiopian region is the only tropical sky island complex that harbored significant glaciation.

Distinctly northern complexes, higher than 40 degrees latitude, include the Altai/Tien Shan and Dzungarian basin ranges; the heavily altered Pyrennes and Scottish Highlands and a fewer other CIS ranges. These areas lost their biota during the glacial periods and have only recently (about 10 to 15,000 years ago) been recolonized.

Along with the Pantepuis, the Brazilian shield, the Great Basin, and most of the Eurasian ranges, the Madrean archipelago is distinctly inland. The Madrean has a special feature—the lowest pass or mountain gap in the Rocky Mountain cordillera between northern Canada and the Isthmus of Tehuantepec. The low elevation pass encouraged east-west movement of animals and plants from valley to valley. Otherwise, the Chihuahuan and Mohave deserts (the desert "seas") and the Gila River geographically isolate the Madrean archipelago. As previously mentioned, the inland configurations are the true sky island complexes. Many of the others are bordered on one side by an ocean or large lakes. Some are surrounded on two sides by ocean. Peninsula sky island complexes have very limited opportunities for colonization because two or three sides are ocean compared to distinctly inland clusters.

The Madrean Archipelago contains a large number of sky islands per complex (N = 40). Only the Great Basin (N = 25 to 50 depending on definition), the East African arc (N = two massifs, about 30 sky islands, and three oceanic islands), and Pantepuis (N = 15 large and about 20 smaller sky islands) have comparable numbers of isolated mountains. Depending on how boundaries are drawn, the Ethiopian complex has two major massifs and about 12 smaller sky islands without the addition of the Horn of Africa mountains and those of Saudi Arabia and Yemen. All other groupings are less than 15 isolated mountains with the majority containing only about five.

In summary, North America's Great Basin and Madrean archipelagos appear unique on the planet for the number of mountains and the stepping stone arrangement between roughly parallel valleys and mountains. Only the Madrean archipelago has the distinct north-south connection to two major cordilleras and crosses from temperate to subtropical latitudes. This topography, relief, and location explain a large part of the biological richness and diversity of the Madrean archipelago.

Table 2.—Geology and the Sky Islands

Type	Examples
Relictual or Subsequent	Most Tepuis (Venezuela)Western Ghats (India)Brazilian shield
Tectonic or Original A. Accumulation mountains (flood basalts, volcanics)	East African arc volcanoes Mt. Camoroun
B. Deformation mountains B1. Fold mountains	Himalayas Andes (altiplano)
B2. Dislocation mountains (horst/graben)	Great Basin Madrean Archipelago African Rift Valley mountains Altai Trans-Baikal
B3. Laccolith mountains	

HOW WERE THE SKY ISLAND COMPLEXES CONSTRUCTED?

The geologic history of each sky island complex provides the stage for its evolutionary and ecological history. The four most important characters are: the nature of the bedrock, the general shape of the mountains and valleys as controlled by erosive and tectonic forces, the timing of mountain building, and the creation and destruction of barriers and bridges to migration of living organisms. Table 2 classifies the sky island complexes by the geologic process which formed the highlands and the topographic relief between valley and mountain (Mani and Giddings, 1980).

The Western Ghats, most of the tepuis, and the Brazilian shield complex are relictual or subsequent mountains, i.e. mountains that started as a plateau and were increasingly dissected by river erosive forces. For instance, the Pantepui's geologic history both constrained and encouraged the rich endemism of its montane flora. The majority of tepuis are hard sandstone with acid lithification (soil-forming properties). Most tepuis are flat-topped mountains (providing more habitat for colonization) with steep cliffs and talus slopes (creating diverse habitats). The evolving flora had to be acidtolerant and, despite the high rainfall, xeric in growth form. The few tepuis of granitic composition were not exceptionally differentiated from the sandstone tepuis. Granite also produces acid-soils. Plant colonization between sandstone and granitic tepuis encountered no immediate "soil barrier."

Tectonic or "original" mountains include mountains (1) built-up by volcanic ash and flood basalts; (2) deformation mountains resulting from continental folding or rifting; and (3) laccolith mountains. I could find no insular laccolithic mountains that were also sky islands.

At least six sky island complexes are combinations of mountain bedrock from volcanic ash and/or flood basalts with subsequent deformation. For instance, the flood basalt mountain cluster of the Ethiopian Highlands was fragmented and gained relief by the sinking of the East African rift valley. Volcanism stopped three to four million years ago, allowing recolonization without further geological disturbance. The Ethiopian highlands are relatively flat-topped (vs. peaked) because of their plateau origin and age. The flatness provided an extensive area for afro-alpine populations to evolve.

Similarly, the Madrean sky islands are deformation mountains from continental rifting that began about 13 million years ago. The mountains did not rise as much as the valleys sank. This 'basin and range" or "horst/graben" development exposed older rocks derived from a highly diverse geologic past: multiple marine invasions, caldera explosions and lava flows, and metamorphic core complexes. "Basin and range" tectonics controlled the parallel valley and mountain sequence so unique to North America and largely shaped the large number of "cradles" of evolutionary differentiation.

As opposed to the Ethiopian complex, each individual Madrean sky island is a remarkable mixture of rock types. Exposed rock types include intrusive igneous rocks (granite), extrusive volcanics (rhyolite, dacite, basalts), metamorphics (gneiss, schists, quartzite), and sedimentary rocks (limestones, shale, conglomerates). For example, the Chiricahua mountains are, in large part, an individual volcano overprinted by Great Basin-type dislocation. The Chiricahuas are the planet's largest recorded volcano whose ash flows contributed to parts of five different sky islands in the Madrean archipelago. In contrast, the Pinalenos, the Santa Catalinas, the Rincons, and the Dragoons are metamorphic core complexes. Each core complex is extensively gneis or granite. Other sky islands are predominantly limestone or various limestones (e.g., Huachucas) and almost all the sky islands have remnant slopes with limestone outcrops.

The Sierra Madre source area for the archipelago is the largest rhyolite mass on the planet with 4,000 foot deep sequences in the Barranca del Cobre. The major Rocky Mountain source area for the archipelago is the Mogollon Rim and Colorado Plateau, one of the largest intact sedimentary sequences on the planet. These relatively flat source areas have been instrumental in feeding colonizing species to the archipelago.

The evolutionary and ecological consequences of this mix of rock types and horst/graben rifting are: (1) a confusing array of piedmont, terrace and valley soils that support a huge diversity of grasses, shrubs, and trees (R. McAuliffe and T. Burgess, this volume); (2) talus slopes which, for instance, support a remarkable diversity of snails (McCord, this volume); (3) limestone slopes and outcrops that greatly increase the diversity of plants on particular sky islands (McLaughlin, 1993 and this volume); and (4) altitudinal limits that extend beyond "typical" climatic zones because of the water holding capacities and heat characteristics of particular rock substrates (Shreve, 1922).

In addition, there are other climatic/geologic derived habitats that increase the floral diversity (e.g., the morainal-related cienagas of the Pinalenos from the last glaciation (Warshall, 1986), the seeps of the Galiuros, the relictual clay valleys of the San Rafael and similar unstudied valleys in Mexico, the aerosol-derived caliche soils of some lower slopes and valleys, and the remnant sand dunes in the Animas, San Simon and other valleys.)

HOW DID IT HAPPEN? BARRIERS, BRIDGES, AND SOURCES

The palaeogeographic history of sky islands has become an exciting and controversial topic. Does stability or instability or what combination of the two generate high levels of biodiversity? Some biologists like to emphasize proximate causes such as the most recent glacial events, the mountain's areal size, ruggedness, exposure, aspect, altitude, distance to nearest sky island, and distance to assumed major source area. Others emphasize the long-term historical framework of planetary palaeogeography. It is beyond the scope of this paper to review sky island speciation theories (see Bush, 1994 for the Amazon region; Journal of African Ecology, 1981 for East Africa).

The Madrean sky islands are uniquely situated in this controversy because all kinds of evidence—pack rat middens, pollen cores, lake sediments, tree rings, fossils, geomorphic surface dating, sea temperatures, radiocarbon and other isotope dating—can be brought forward to argue for various driving forces toward increased speciation. In the southwest, the history of winter vs. summer rainfall and the decoupled influences of temperature vs. rainfall can help explain when the valley vegetation was a barrier that restricted gene flow or when the valleys were bridges that encouraged gene flow.

From a partial review of the literature of the planet's sky islands available in English, I would like to summarize a few lessons. First, sky island species richness can have complex sources and migration routes. For instance, *Bursera is* an African genus that migrated through Laurasia and across North America to the present southwest in the upper Cretaceous/Eocene (Sousa, 1993). Other plants colonized the archipelago after the Panama landbridge connection (Wendt, 1993). A simple model based on changing precipitation and/or temperature for the last glacial period can only explain a small part of the Madrean archipelago's diversity and richness.

Second, the richness of certain Madrean taxa (e.g., flightless beetles, talus snails) may be better explained by the down-falling of the valleys with subsequent vicariant allopatry than by climatic/vegetation flux. Third, other types of barriers and bridges besides valley vegetation occur (Table 3). These include the Pleistocene lakes such as Cochise Lake in the Wilcox playa, the ancient Gila River which was connected to the Yaqui River, and the presence of extensive alluvial fans and roaring rivers in the Pleistocene. These river/lake barriers and bridges are essential in describing the diversity of fish in the Madrean archipelago (Hendrickson, 1980). Fourth, there is a complex interaction between vertical and aspect migration on each individual mountain, the genetic/phenotypic plasticity of the taxa, speciation rates, and climatic/vegetation change. Certain sky islands have provided "safe sites" for organisms because of their latitude and topography. Some sky islands have more frequent colonization attempts because of riparian corridors or valley configuration. Still other sky islands have maintained and added diversity because the invading flora and/or flora had great phenotypic or genotypic plasticity (e.g., *Erigeron).* These complex interactions await researchers.

Table 3.—Sky Island Bridges and Barriers.

Bridges	Barriers
River and river systems	Riparian systems in arid lands
Lakes	Stepping stones (hills, mts.)
Coastlines	Wind, water, and animal dispersal
High altitude cordilleras	Valleys/gaps with favorable soils climat or ecology
Valleys with alien climate, soils or ecology	Alluvial fans (?) in arid lands Phenotypic/genotypic plasticity

Nevertheless, the Madrean archipelago indicates that regions of maximal disturbance (vs. maximal stability) can encourage species richness, if not endemism, in particular taxonomic groups. The continental position of the archipelago and its relation to three major storm fronts can only have created highly erratic rainfall and temperature regimes. In the past two million years, 15 to 20 glacial fluxes (each about 90,000 years) with short "reprieves" lasting 10 to 15,000 years have influenced the biodiversity of the archipelago. The Madrean archipelago has been spared the "wipe out" experienced by sky island complexes of more northern latitudes (e.g., Eurasian) where the glaciers covered the land's surface. Only the Pinaleno mountains appears to have experienced a small montane glacier.

LIFE ON THE MADREAN SKY ISLANDS

Sky island complexes tend to have greater species richness, greater endemism, more clinal variation, more biogeographical specialties, and unique cultivars compared to other inland terrains. A comparison of planetwide sky island diversity is beyond the scope of this paper. Instead, I will briefly describe the "big picture" of biodiversity in the Madrean archipelago. McLaughlin (this volume) provides more detail on the flora.

The Sierra Madre of Mexico, the Madrean archipelago and other outlier sky islands have been identified as one of the three "megadiversity" centers of the planet. It is the only group of sky islands straddling two major floristic (the Neotropic/Holarctic) and two faunal realms (Neotropic/Nearctic) on the planet (Walter, 1979). The Ethiopian complex borders two faunal province boundaries but lies within one floristic realm. The Drakenbergs and other South African sky islands are associated with the unique Capensis floristic realm which partially explains the regions outstanding number of floral endemics (Takhtajan, 1986).

Reflecting this floristic/faunal straddle and the relatively recent landbridge between North and South America, the Madrean archipelago and its two immediate sources areas contain the biogeographic limits of 14 plant families (northern limit); 11 bird families (seven at their southern limit; four at their northern limit), 30 bird, over 35 reptile, and about 15 mammal species. The bioregion supports the second highest plant endemism between the Pacific coast and the Great plains (McLaughlin, this volume). Sixty percent or more of the plants of the dry forest, oak/pine woodlands, and deserts are probably endemic (Rzedowski, 1993). Similarly, the ant fauna (S. Cover, this volume), the lichens, the snails, the reptiles, the birds, and the mammals show exceptional species richness and/or endemism. The bioregion is considered the most diverse sector of the United States for ants, mammals and reptiles.

The archipelago harbors many poorly studied groups (e.g., Buchman, this volume; Carl Olson, personal communication) and many taxonomically confusing groups (e.g., McCord, this volume). But, as opposed to other regions, detailed systematic investigations have led to more species or subspecies ("splitting"), not fewer ("lumping"). For instance, *Erigeron pringlei,* a local fleabane, on detailed investigation, was split into four species, including a new endemic to the Pinalenos *(E. heliographus).* A new frog was recently discovered in Ramsey Canyon *(Rana subaguavocalis).* The Mt. Graham red squirrel *(Tamasciuris hudsonicus grahamensis),* previously considered one of twenty-six subspecies, now appears increasingly unique.

The Madrean archipelago is the planet's center for the long coevolutionary history of several species groups. The coevolution of squirrels, woodpeckers, jays and one parrot, the woodland's mycorrhizal, epigeous and hypogeous mushrooms and truffles (States, 1992) centers in the Madrean pine/oak woodlands. The coevolution of agaves with bats and hummingbirds centers in the semi-desert grasslands and thornscrub.

There are innumerable mysteries: Why do some localities have only pines or only oaks, while others have pine/oak woodland? Why are there no chipmunks on the Huachucas? Why does the Mexican chickadee *(Parts sclateri)* stop at the Chiricahuas and not cross the 35 miles to the Pinalenos where the Mt. Chickadee (P. *gambeli)* starts? How have the talus snails coevolved with the varied rock substrates and lichens of the individual sky islands? Why does it appear that many southern mammals have expanded into the northern sky islands and beyond in the last half-century? How important is vertical migration up-and-down slope and from the flanks into the valley toward maintaining population stability?

SUMMARY

From a planetary point of view, the Madrean sky island archipelago has these unique features:

- It is an archipelago between two cordilleras (the Sierra Madre Occidental and the Rocky Mountains);
- The archipelago contains an extraordinary number of sky islands per complex;
- The complex has a north-south axis spanning about eight degrees of latitude but contains a distinct east-west valley bridge through the Deming Gap of the Rocky Mountains;
- The islands have a mixed geological composition apparently unrivaled in other areas of the planet;
- The islands have a moderate to high relief (5,000 feet) compared to other valley/mountain complexes with the obvious exceptions of the Himalayas and Andes;
- The Madrean archipelago is the only sky island complex to straddle two major floristic and two major faunal realms as well as the convergence of three major climatic zones (tropical, subtropical, and temperate);

Its mid-latitude position placed it at the edge of glacial influences without experiencing any of the mass extinctions that occurred in the sky island complexes of the more northern latitudes;

The Madrean archipelago endemism and species richness probably reflects a palaeogeographic history in which maximal disturbance with a large turnover of species (e.g., the Pleistocene megafauna) produces great biodiversity, It is not a region of maximal stability.

I have not mentioned one major influence on the planet's sky islands - humans. The influence of Iron Age deforestation and the spread of domestic livestock have permanently changed many sky island valleys and mountains. The Horn of Africa, for instance, has had livestock since 5,000 BC. The Mediterranean mountains have experienced livestock and significant treecutting since about 1,000 BC. The loss of diversity cannot be retrieved or fully known in sky island groups such as the Pyrennes, the Atlas Mountains of Morocco, or the Cabal Lubnan of Lebanon. The Madrean archipelago and its admirers are lucky. Major Iron Age and domestic livestock influences on the Madrean archipelago started less than 200 years ago.

However, the pace and intensity of human influence has been accelerating. 150 species of concern—species listed as vulnerable—dwell within the sky island archipelago, excluding bats (Warshall, in press; Sky Island Alliance, 1992). The jaguar, grizzly, ocelot and graywolf have been extirpated from the United States portion of the archipelago and are probably extirpated from the Mexican portion. Genetic swamping or replacement from translocated species (e.g., hybridization of rainbow and Apache trout, *Salmo gairdneri X Oncorhynchus apache;)*; invasion by over sixty non-native plants which have naturalized and degraded valley and desert vegetation (E. Pierson and J. McAuliffe, this volume); long-term declines of some game species, especially band-tailed pigeons *(Columba fasciata)*; and urban pressure that has fragmented, if not eliminated, the corridors between various sky islands are clear and present harms.

Policy and attitudes concerning livestock raising and fire management are in a state of flux with attempts to understand "more natural" or "better" or "more balanced" management practices. Piecemeal destruction of both the remaining forest and aquatic habitats is a major concern in both the Coronado Forest and in Mexico. Increasingly, Mexico and the United States realize that some problems and some solutions are international. Binational inventories of the sky island flora and fauna will require close cooperation among scientists and meetings like the present conference. Mexico remains the best source for some animals that are now near extinction in the United States (e.g., black-tailed prairie dog, *Cynomys ludovicianus,* or thick-billed parrot, *Rhynchopsitta pachyrhyncha)* and cross-border cooperation may be necessary to reintroduce the Mexican wolf, *Canis lupus baileyi,* manage various races of pronghorn as well as migratory birds, bats, and butterflies. In short, to conserve both nations' unique natural heritage, a deep commitment to preserving minimal viable habitats for resident and migratory species is paramount. Part of this effort is understanding the unique position of the sky island archipelago in the Earth's family of continental island ecosystems.

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