NORTH AMERICA,
PATTERNS OF
BIODIVERSITY IN

Martin J. Lechowicz
McGill University

I. Continental Diversity
II. Terrestrial Bioregions of North America
III. Diversity in Major Groups of Organisms
IV. Changes in North American Biodiversity
V. Conclusion

GLOSSARY

Beringia A region at the northwestern corner of North America separated from Asia only by the shallow waters of the Bering Strait. When ocean levels drop during glaciation, Asia and North America are connected by land in this region.

bioregion A landscape subunit at the scale of the continent that is set apart by its coherent geological and biotic history.

continental shelf The continental margin, which is submerged to depths to approximately 180 m at current sea levels and is bounded by the abrupt drop to the abyssal depths of the oceans.

ecoregion A landscape unit within a bioregion in which a distinct assemblage of organisms interact ecologically, usually within a spatial context defined by drainage systems, mountain ranges, or similar natural boundaries.

Holartic A biotic realm in the temperate, boreal, and arctic regions of the Northern Hemisphere with strong affinities among the regional floras and faunas.

Neotropics A biotic realm in tropical South and Central America with strong affinities among the regional floras and faunas but different from the tropical biota of Africa and Southeast Asia (the Paleotropics).

physiography The landforms that give shape and character to the continental landscape, for example, the configuration of mountains and drainage basins.

THE DIVERSITY OF THE FLORA AND FAUNA OF NORTH AMERICA has been the focus of study by naturalists and scientists for the past few hundred years. Studies of species diversity have proceeded even as parts of North America have undergone dramatic changes driven by activities associated with settlement, mining, forestry, agriculture, and industrial development. Large areas of the midcontinent have less than 5% of their primeval landscape intact. This article attempts to identify the patterns of species diversity that existed in North America 500–1000 years ago, before the arrival of the Europeans. The focus is on the diversity and distribution of native or indigenous species, as opposed to species that people have introduced from other places. Current or historical records from relatively undisturbed habitats provide the basis for estimates of species diversity from region to region. This article is restricted to the diversity of the terrestrial and freshwater biota of mainland North America, including offshore islands but excluding the rich marine biota associated with the continental shelf and coastal estuaries. Although the continental shelf is quite properly considered part of
North America, its biota is determined not only by continental but also oceanic influences of considerable complexity. The evaluation and summary of North American marine diversity is a separate and important task, but it is beyond the scope of this article.

I. CONTINENTAL DIVERSITY

Mainland North America, with an area of 24,258,000 km², accounts for 16% of the land surface on Earth and stretches over 65° of latitude. The ancient core of North America is well over 3 billion years old, but parts of the continent are much younger. The continent is bounded on the west by a series of mountain ranges along the coast of the Pacific Ocean. A more extensive coastal plain and less rugged mountains characterize the Atlantic coast of North America. The Arctic Ocean lies at the northern limit of the continent, which includes the extensive Arctic Archipelago. Rugged mountains mark the commonly accepted limit of the continent in southern Mexico, but in fact distinguishing the boundary in this mountainous and geologically complex region where North America grades into Central America is arbitrary. The continental interior is an extensive plain with relatively little topographic relief, although highlands, escarpments, and erosional features occur regionally. Major drainage systems flow both north and south from the interior and also through the Great Lakes basin to the east. The Mississippi River system flowing south into the Gulf of Mexico is among the largest drainage basins in the world. The Caribbean Sea lies southeast of the continent. North America has a land connection to South America through the Isthmus of Panama, a link that formed only approximately 3 million years ago (Ma). In the past few million years, as ocean levels have fluctuated during glacial cycles, there has also been an intermittent land connection to Asia through Beringia. People arrived in North America by this route, and perhaps others, only very recently—sometime in the past 15,000–35,000 years. With the exception of Antarctica, the Americas were the last of the continents to be colonized by people. Although recently much influenced by people, the biota of North America evolved for hundreds of millions of years without a human presence. The current diversity of the continental biota is founded on this long period of geological and evolutionary history.

Two biological processes interact over millions of years in the evolutionary history of the continental biota: speciation and extinction. Populations, isolated from one another by changing landforms or climates, diverge to form new species. Species go extinct in the face of changing environments or by chance events in small populations. The number of species in a continental biota at any point in time reflects in part an ongoing balance between speciation and extinction on the continent as a whole. The evolutionary history of a continent is intimately interwoven with its geological history, especially through the influence of continental drift. In the 400 million years since life appeared on land, interchange among different continental biotas has been possible whenever continents have drifted into contact with one another. Species that have evolved separately on other continents have had opportunities to disperse and colonize North America. This occasional mixing of continental biota together with in situ evolution in North America has created the total pool of species on the continent today.

Although this pool of species defines the current magnitude of diversity in North America, the regional patterns of diversity are set by the different distributions of individual species within the continent. Some regions have more species, and others have fewer. The range of a species within a continent reflects both environmental requirements and the ability to disperse to suitable environments. Species differ in their rates of dispersal and establishment in the face of changing environments and in their ability to cross barriers such as mountains, bodies of water, or inhospitable habitat. The physiography of the continent is thus an important influence on the current patterns of species diversity within North America. Species distributions also depend on climatic patterns within the continent, which arise from both the local influence of physiographic features and the global patterns of atmospheric circulation from season to season. In the end, the complement of species found in a region depends on the ability of species to disperse to the region, establish there, and survive and reproduce there. Ecological processes acting on relatively short timescales (years to millennia) are the proximate controls on species distribution, but the availability of the species and the distribution of suitable habitats on the continent ultimately have arisen in geological and evolutionary processes acting over much longer timescales (millions of years). It is this interplay of processes on ecological and evolutionary timescales that effects the natural patterns of diversity in North America.

II. TERRESTRIAL BIOREGIONS OF NORTH AMERICA

Mainland North America and its offshore islands can be divided into six bioregions: (i) the Canadian Shield
in the north, (ii) eastern North America, (iii) western North America, (iv) southwestern North America, (v) a northern extension of the Central American biota in southern Mexico, and (vi) outliers of the Caribbean biota on the southern tip of the Florida peninsula. Figure 1 illustrates and depicts in a general way the boundaries of these six terrestrial bioregions in North America. There is, of course, substantial physiographic and biotic diversity within each bioregion, and the boundaries between adjacent bioregions are not precisely identifiable. Fairly distinct ecoregions can be recognized at smaller spatial scales within each bioregion, and these are important for understanding and conserving biodiversity (Abell et al., 1999; Ricketts et al., 1999). Larger drainage systems, such as that of the Mississippi River and its tributaries or the Great Lakes basin, subsume many terrestrial ecoregions. The geography of the terrestrial versus freshwater biota of North America differs at the scale of ecoregions and to some degree at the scale of the continental bioregions. Similarly, the recognition of bioregion boundaries at the current continental margins is arbitrary. Continental watersheds are directly linked ecologically to the marine diversity of the continental shelf, and this shelf typically shares a geological history with the adjacent continent. Despite these uncertainties in the boundaries and internal structure of the six bioregions, each does have a reasonable coherence in its geological history, current physiography, and current biota. These bioregions therefore provide a useful working framework in which to summarize the general patterns of terrestrial and freshwater species diversity within North America.

The first three of these bioregions are part of the Holarctic, a zonal assemblage of flora and fauna that has coherence across the whole of the middle and higher latitudes of the Northern Hemisphere. Species may differ among North America, Europe, and Asia, but many families and genera of plants and animals are represented throughout the Holarctic. Higher latitudes within the Holarctic realm, including the Canadian Shield, have especially strong biotic affinities. High-latitude sites in North America, Europe, and Asia are
in close proximity around the polar region and share common climatic regimes; biota can disperse and establish among these high-latitude regions more easily than they can move between the more distant and climatically disparate latitudinal extremes within North America. The biota at midlatitudes in the Holarctic, on the other hand, are more strongly influenced by longitudinal climatic gradients and longitudinal contrasts in geologic history and physiography. Hence, we distinguish eastern and western bioregions in the mid-latitudes of North America, whereas the Canadian Shield bioregion stretches across the top of the entire continent. Some biogeographers, recognizing similar longitudinal differences at midlatitudes on a global scale, divide the Holarctic into the Nearctic and Paleartic regions. North America comprises the Nearctic.

The last three North American bioregions have strong affinities with the Neotropics, the biotic realm to which South America belongs. The biota of equatorial regions do not have the global coherence that characterizes the Holarctic. Tropical regions of Africa and Southeast Asia, which have a flora and fauna that is distinct from that in the Neotropics, are distinguished as the Paleotropics. The Caribbean and southernmost North American bioregions are unambiguously Neotropical, basically representing the northern extent of floras and faunas centered on the continent of South America. The southwestern North American bioregion, on the other hand, is a mix of Neotropic and Holarctic biota and is one of the most species-rich regions in the world.

A. Canadian Shield

This bioregion takes its name from the Canadian Shield, which is the ancient core, or craton, of the North American continent. The bioregion and the craton are not geographically identical. The craton extends as basement rock well under the central and eastern parts of the continent, but this does not affect the regional development of the modern biota. The southern boundary of this bioregion is marked by the shift in surface geology from the ancient, crystalline bedrocks of the craton to younger, sedimentary bedrocks. The bioregion actually extends beyond the craton in northern Alaska and the Yukon, even though the bedrock in these western regions is not nearly as ancient. Two major biomes occur with the Canadian Shield bioregion: the boreal forest and the arctic tundra.

Tundra occupies the coasts and islands of the Arctic Ocean and higher elevations in interior Alaska and the Yukon. These barren lands with a short, cold growing season are relatively poor in plant and animal species. From one ecoregion to another within the Canadian Shield bioregion, there are only 100–750 plant species in tundra. Some tundra ecotones have as many as 50 mammal and 160 bird species, and from 0 to 75 butterfly species, but very few have any reptile or amphibian species. There are usually only approximately 5–25 fish species in tundra. Tundra diversity decreases seasonally as birds migrate to more southern bioregions for the winter. The most diverse tundra biota occurs at high elevations in the Wrangell–St. Elias Range in southern Alaska and the adjacent Yukon. The least diverse tundra occurs along the coasts of the heavily glaciated Axel Heiberg and Ellesmere Islands, both of which extend north of 80° N latitude. There are only approximately 110 species of vascular plants in this northernmost part of North America.

The boreal forest, which occupies the more southern parts of the Canadian Shield bioregion, generally has greater biodiversity than the tundra. Different boreal ecoregions have between 250 and 1250 vascular plant species that include 5–30 tree species. There are never more than 10 coniferous tree species in any ecoregion, even though conifers dominate much of the boreal landscape. Ecoregions in the boreal forest usually have approximately 20–50 mammal species, 105–185 bird species, 35–95 butterfly species, and 20–60 fish species. Amphibians are less diverse, usually 1–5 species in an ecoregion and occasionally more than 10; there may be 1–3 reptile species, but often there are none in a given ecoregion. The boreal forests of central and eastern Canada are the most diverse overall, and those of Newfoundland are the least diverse.

B. Eastern North America

The Appalachian Orogeny essentially created the character of this bioregion. These mountains on the eastern margin of North America arose approximately 300 Ma in the collision of all the ancient continents to form the supercontinent Pangea. The Appalachians are in fact a part of the African continent left behind as the mid-Atlantic Rift developed beginning approximately 240 Ma, gradually breaking up Pangea, creating the Atlantic Ocean and moving Europe, Africa, and the Americas to their current geographic positions. As the young and rugged Appalachians eroded, huge deposits of sediment accumulated in the continental interior forming the bedrock of much of the interior plains that comprise the central part of this bioregion. Their sedimentary deposits also account for an extensive continental shelf, rich in marine biota today and also an important corridor for plant and animal migrations during and after glacial
peaks when ocean levels are low. From approximately 170 to 70 Ma much of the more western interior of this bioregion lay beneath shallow continental seas in which marine biota built up extensive reef systems and sediments. The Canadian Shield forms the basement rock of essentially the entire bioregion, but it is these much younger mountains and sedimentary features that influence the current patterns of biodiversity.

The eastern parts of this bioregion are generally forested with some combination of conifer and broadleaf trees. The western parts are more often grasslands, except for gallery forests along watercourses. The transition from forest to grasslands, which is more a mosaic dependent on local topography and drainage than a smooth gradient, generally occurs to one side or the other of the Mississippi River. Savannas, grasslands with a scattering of trees, are common in the transitional ecoregions. Many of these transitional ecoregions, such as the Edwards Plateau in Texas, have exceptionally high biodiversity. There are approximately 650–3350 species of plants in the different ecoregions of eastern North America, 30–85 mammals, 160–270 birds, 5–65 amphibians, 5–85 reptiles, 75–230 butterflies, 40–230 fish species, 2–260 land snails, 5–125 mussel species, and 1–65 crayfish. The mixed forests of the southeastern United States comprise the ecoregion most rich in plant species within eastern North America, and the Pine Barrens of the Atlantic Coastal Plain are the least rich. The western short grasslands are richest in mammal species, and the Florida Pine Scrub is the least rich. These western short grasslands also have the most butterfly species in this bioregion, whereas the lowland forests of the Gulf of St. Lawrence have the least. The grasslands of the western coast of the Gulf of Mexico are most rich in bird species, and the Nebraska Sand Hills are least rich. Very high numbers of both amphibian and land snail species occur in the forested Blue Ridge and southern Appalachian Mountains. The Tennessee and Cumberland River systems, which drain the unglaciated Appalachian–Blue Ridge region, are the most rich in fish, mussel, and crayfish species of any region in the bioregion; the glaciated, northern parts of the bioregion are most poor in freshwater biota.

C. Western North America

Western North America is younger and more rugged than the northern and eastern parts of the continent, with some coastal mountains having been created only in the past 1 million years. All of western North America was created as the Farallon Plate, which has been squeezed between the Pacific and North American Plates, gradually subducted under the North American Plate. The subduction of the Farallon Plate caused a series of major episodes of mountain building in western North America: the Sonoran Orogeny approximately 245 Ma, the Nevadan Orogeny approximately 150 Ma, the Sevier Orogeny approximately 120–90 Ma, the Laramide Orogeny approximately 70–60 Ma, and the Basin and Range Orogeny approximately 15 Ma. The continued subduction of the Juan de Fuca Plate, a remnant of the now broken up Farallon Plate, accounts for the current geologic activity in the Pacific Northwest. All this mountain building associated with the expansion of the North American continent has created and defined the essential character of this bioregion. The landscape is physiographically diverse, with a high degree of regional isolation leading to many distinct ecoregions and a biota rich in local endemics.

The mountains that dominate the landscape in the bioregion are predominantly forested, but various grasslands, shrublands, and deserts occur in basins and on plateaus amid the mountains. Between ecoregions, there is considerable variation in species diversity. There are approximately 450–2550 species of plants in the different ecoregions of western North America, 30–110 mammals, 140–240 birds, 1–20 amphibians, 0–90 reptiles, 5–225 butterflies, 0–50 land snails, 5–60 fishes, 1–5 mussels, and 0–5 crayfish. Plant species diversity is lowest on the isolated Queen Charlotte Islands and high in the Sierra Nevada, in the Great Basin, and on the Colorado Plateau. The Colorado Plateau and the Sierra Nevadas are notably rich in bird species. The Colorado Plateau and the Colorado Rocky Mountains are rich in butterfly species, whereas the Queen Charlotte Islands are very poor in butterfly species. The forested coastal mountains have the most amphibians in the bioregion, and the Colorado Plateau and the Great Basin have the most reptile species. The Siskiyou Mountains, the Sierra Nevada, and the north Central Rocky Mountains are all notably rich in species of land snails. Although low in terrestrial biodiversity within the bioregion, the watersheds of the mountains along the northern Pacific Coast are the most rich in aquatic species; the isolated and arid watershed of south-central Oregon is the least rich. The Colorado Plateau shrublands are the most species-rich ecoregion overall, whereas the Queen Charlotte Islands and the adjacent northern Pacific Coast are the most species poor.

D. Southwestern North America

Northern and central Mexico and immediately adjacent parts of the American Southwest form a distinct biore-
region within North America, which like western North America has rugged and relatively young terrain. The Sierra Madre Occidental and Sierra Madre Oriental running down the western and eastern coasts converge on a belt of high mountains of volcanic origin in southern Mexico, which form a natural boundary at the southern limits of this bioregion. These mountainous regions surround an interior plateau that grades north into increasingly arid deserts. The mountain ranges stand in contrast to the low relief of the coastal plains along the Pacific Ocean and the Gulf of Mexico and to the Baja California Peninsula. Ecoregions in southwestern North America are especially rich in bird, mammal, reptile, and butterfly species. Among the ecoregions, bird species number 90–280, mammals 50–110, reptiles 10–105, fishes 10–50, and there are at least 130–260 butterflies. Numbers of plant species are also high—1500–4000 species among the ecoregions—but there are as many as 8000 species along the Sierra Madre Oriental. Not surprisingly given the aridity of this bioregion in general, the diversity of amphibians is low—only 5–20 species in most ecoregions. There are insufficient data to designate an ecoregion that is the most rich in biodiversity overall, but the more diverse ecoregions are almost certainly in Mexico as opposed to the southwestern United States.

**E. Southernmost North America**

The tropical highlands of the Sierra Madre del Sur and the Sierra Madre de Chiapas and the tropical lowlands on the Pacific and Gulf Coasts of Mexico comprise this bioregion, which is located at the southern limits of North America. This part of North America has a complex and poorly understood geological history involving the convergence of five plates and various crustal fragments of uncertain continental affinity. It appears certain, however, that the rugged mountains of Central America and the land connection between North and South America have developed only in the past 2–5 Ma. For the preceding 70 Ma or more, North and South America had been separated by an ocean channel deep and wide enough to severely limit biotic exchange between the two continents. Once Central America arose as a bridge between the two continents, its biota was enriched by migrations in both directions, but especially by Neotropical flora and fauna from South America that were well-suited to its tropical climate. Most ecoregions in this part of southern Mexico have on the order of 8000 plant species, although this decreases to only approximately 2000 on the Yucatan Peninsula where water quickly drains deep underground in the karst landscape. Some ecoregions have as many as 125 amphibian species, but most have only 10–30. Many ecoregions have as many as 120–160 reptile species, 100–300 bird species, and 80–160 mammal species. The overall diversity of this bioregion is high and increases toward the south as the influence of the South American biota strengthens. Defining the southern limit of North America at the Isthmus of Panama would greatly increase the biodiversity of the continent as a whole.

**F. Caribbean**

The Caribbean Plate has a poorly understood geological history. Most of the plate is submerged in a shallow sea dotted with island arcs that are closest to North America at the Florida Peninsula. The southern tip of Florida, the only part of North America that is located in the Caribbean bioregion, has a biota that is a mix of continental and Caribbean elements. There are approximately 1000 species of plants, 25 species of mammals, 175–200 species of birds, 15–20 species of amphibians, 45–50 species of reptiles, 130–135 species of butterflies, and 60–65 species of land snails. Despite the addition of Caribbean species, the biota is not exceptionally rich compared to adjacent parts of the continent.

**III. DIVERSITY IN MAJOR GROUPS OF ORGANISMS**

An alternative perspective on the general levels and patterns of biodiversity in North America is to focus on the distribution of species in particular taxonomic or functional groups of organisms. Although our knowledge of the biodiversity of North America is better than that for many other parts of the world, it is far from complete and we can only adopt this perspective for the better studied organisms in North America. A few groups of vertebrate animals are fairly well studied, but the diversity of even these is poorly known in parts of Mexico. Some groups of insects and vascular plants are fairly well studied throughout the continent, but the sheer numbers of species in these groups undoubtedly indicate that many have yet to be discovered and properly mapped. Well-founded summaries of diversity in microbial groups, many invertebrate animals, fungi, and nonvascular plants currently do not exist for North America as a whole. Despite our incomplete knowledge of North American diversity in individual groups of organisms, the numbers of species and distributional patterns in the better known groups yield insights and provide guidance for conservation efforts.
A. Plants

There are approximately 1320 species of mosses in North America north of Mexico and approximately 1200 species known from Mexico. The liverworts and hornworts in North America north of Mexico number approximately 650 species, with about 800 species known from Mexico. All these numbers are expected to increase as the continental bryoflora is better explored. There is no comprehensive North American flora for these plant groups.

The pteridophytes (ferns, horsetails, club mosses, spike mosses, and quillworts) are among the most primitive vascular plants represented in the North American flora. There are approximately 440 species of pteridophytes in North America north of Mexico, more than 75% of which are ferns. Mexico has on the order of 1000 pteridophytes species, most of which are ferns of moist habitats and Neotropical affinity. For example, there are only approximately 125 pteridophyte species in the Chihuahuan Desert of northern Mexico compared to almost 700 species in the southern state of Oaxaca. The moist, tropical forests of southern Mexico harbor the greatest diversity of pteridophytes in North America.

The gymnosperms, an ancient group of plants that includes the pines, spruces, and other conifers, are commercially important and especially well-known in North America. There are approximately 90 conifer species in North America north of Mexico; numbers of conifers in Mexico are higher but uncertain. The well-studied pines of Mexico offer one specific point of comparison to the rest of North America. There are approximately 35 pine species in North America north of Mexico, and only about one-third of these have ranges extending into Mexico. There are another 60 species of pine in Mexico! On the other hand, there are 11 spruce species in North America, but only 2 occur in Mexico. The frequently isolated, arid mountain habitats of Mexico clearly have provided a center for the evolutionary diversification of pines in North America. North of Mexico the greatest concentration of conifer species is found in the Klamath–Siskiyou ecoregion on the mountainous coast at the California–Oregon border; approximately 30 species of conifer are found there. Conifer diversity is generally greater in the western mountains than in eastern or northern North America.

Trees in general, angiosperm as well as gymnosperm species, are well studied in North America. There are approximately 650 native species of trees in North America north of Mexico, approximately 85% of which are angiosperms; the arboreal flora of Mexico is not known with certainty but there are at least as many, and probably substantially more, tree species as there are in the rest of the continent. The oaks, which are well studied in North America including Mexico, provide a useful point of comparison. As many as 150 species of oaks are known from Mexico, approximately 30 of which are also found farther north. There are only about 60 additional oak species in the rest of North America. The Mexican oaks predominate in arid habitats, with the mountains of central and eastern Mexico being a center of diversity. The center of tree diversity north of Mexico is in the southeastern United States, where as many as 190 tree species can be found in a given ecoregion. With the exception of Mexico, the diversity of hardwood species declines steadily to the west and north of this concentration of species in the southeastern United States.

The angiosperms, both herbaceous and woody, are the most recently evolved and most species rich of the vascular plant groups in North America and indeed throughout the world. The angiosperms comprise the largest part by far of any regional flora. They are also the least completely identified and mapped in terms of their North American patterns of biodiversity. There is no comprehensive floristic inventory for North America, only a series of regional descriptions. There may be as many as 17,000–20,000 native plant species in North America north of Mexico. At midlatitudes, the highest diversity of angiosperm species in an ecoregion is in the forests of the southeastern United States, where there are approximately 3000 native angiosperms; species diversity decreases to the west and north on the continent but increases dramatically in Mexico. The state of California, which includes many diverse ecoregions, has more than 5000 native plant species. The whole of Canada has about only 3125 native angiosperm species, and the Canadian Arctic Archipelago has only 330. Mexico, on the other hand, has approximately 19,000 angiosperm species; the state of Oaxaca alone has about 8000. Mexico has approximately 2600 of the 5500 species in the Asteraceae (sunflower family); there are only 400 native species of Asteraceae in Canada. The Fabaceae (bean family) has approximately 1700 species in Mexico, with more than half occurring only in Mexico, compared to only about 130 in Canada. The 900 species of Cactaceae (cacti) in Mexico represent more than half the species in the world. The greatest angiosperm diversity in North America is clearly found at the southern end of the continent.
B. Butterflies
There is no reliable estimate of the total number of butterfly species in North America. Comprehensive surveys of western and southwestern North America report only approximately 530 species of butterflies, although this is believed to be from the part of the continent north of Mexico where butterfly diversity is greatest. Surveys of remnant prairie in the midcontinent yielded only approximately 90 species of butterflies, but the prairie ecosystems have been much disrupted in the past 200 years. There are estimated to be approximately 2200 butterfly species in Mexico, and it is certain that butterfly diversity within North America is greatest in Mexico. The swallowtails (Papilionidae), which are among the more conspicuous and better known butterflies, provide evidence of the relative richness of the Mexican butterfly fauna. There are almost 60 swallowtail species in Mexico, about twice as many as in the more northern parts of the continent.

C. Land Mammals
There are approximately 4500 mammal species in the world. Canada has approximately 140 species of mammals, whereas the United States has about 350 and Mexico about 440–450. There is no good composite estimate for the continent as a whole. North of Mexico, the Colorado Plateau harbors the greatest diversity of mammal species but the Chihuahuan Desert, which extends into Mexico, is equally rich in mammal species. The species richness of mammals in North America decreases steadily to the north, and at midlatitudes it is relatively low in the east compared to the west.

D. Birds
There are approximately 9000 bird species in the world. Canada has approximately 425 species of birds, the United States approximately 650 species, and Mexico approximately 960–1050 species. There is no good composite estimate for the number of bird species on the continent as a whole. The geographic pattern of species richness for birds in North America is generally similar to that of mammals: richest in Mexico and the adjacent southwestern United States and steadily decreasing to the north.

E. Amphibians
The amphibians in North America primarily include frogs and salamanders. There are approximately 4000 amphibian species in the world. Canada has approximately 40 species of amphibians, none of which do not also occur farther south on the continent. Mexico, in contrast, has approximately 285 amphibian species, approximately 170 of which do not occur elsewhere in North America. The United States has approximately 230 amphibian species. There is no good estimate of the number of amphibian species for the continent as a whole. With 55–70 amphibian species, the Appalachian Mountains comprise the region north of Mexico that is most rich in amphibian species, but this is only one-fourth of the number of species in the tropical highlands of central and southern Mexico.

F. Reptiles
The reptiles in North America include turtles, lizards, snakes, and a negligible number of crocodilians. There are about 6000 reptile species in the world. Canada has only about 40 species of reptiles, none of which do not also occur farther south on the continent. The United States has approximately 280 species of reptiles. Mexico has about 690–720 reptile species, approximately 370 of which do not occur elsewhere in North America. The Chihuahuan Desert is the part of the continent most rich in reptiles.

G. Freshwater Fishes
North America has approximately 1200 species of freshwater fish. There is, however, substantial variation in the diversity of fishes in glaciated and unglaciated parts of the continent. The glaciated regions are notably poor in fish species. Canada, despite its very large land area rich in lakes and river systems, has only approximately 180 native fish species. The extensive Hudson Bay Basin, which was entirely glaciated 18,000 years ago, has only approximately 100 fish species and most of these occur in the southern headwaters of the drainage system. The Canadian Arctic Archipelago has fewer than 10 fish species. In contrast, the largely unglaciated Mississippi River Basin has approximately 375 fish species. The southeastern United States has 485 freshwater fish species, with the greatest diversity in the Appalachian and adjacent Interior Plateau. Despite the aridity of much of Mexico, about 380–500 freshwater fish species occur there, with notably high numbers of species in the Panuco and Papaloapan River systems along the southwestern coast of the Gulf of Mexico. The arid regions of southwestern North America had wetter climates and more extensive wetland systems as recently as 7500 years ago, but the fish fauna now is restricted
to remnant bodies of permanent water. Although the habitats available for fishes in southwestern North America are currently limited, there are many remnant species with a high degree of endemism.

IV. CHANGES IN NORTH AMERICAN BIODIVERSITY

There is a long history of patterns of biodiversity in North America. The native species that occupy North America today belong to groups of organisms that have developed over the long history of life on this continent. Some of the earliest life on land is represented by fossil plants more than 400 million years old that are found along the Acadian coast of North America. The continent has shared in the evolutionary diversification of life on land. Ancestors of conifers in the family Pinaceae grew in what is now North America 135 Ma. Angiosperm fossils from North America date to approximately 120 Ma, near the origins of this now dominant group of plants. Dinosaurs that dominated the animal life of North America beginning approximately 200 Ma are ancestors to the modern birds; the mammals rose to dominance beginning 65 Ma with the mass extinction of dinosaurs. Primitive insects are among the earliest fossils of terrestrial life in North America, but the rapid increases in species numbers of groups such as the butterflies and beetles that have high diversity in North America today also began only 65 Ma. Patterns of continental drift and climate change during the 400 million years that life has been on land have facilitated the exchange of biota from different continents. The strong affinity in the flora and fauna of the Holarctic regions of North America, Europe, and Asia has its origins in the period 170–80 Ma, when these continents were still in close proximity to one another. Similarly, the richness of the Central American flora and fauna in southernmost North America stems in part from biotic exchanges initiated in the past 2 or 3 Ma when the Americas were reconnected by land after 60–70 million years of relative isolation from one another. Some contemporary patterns of diversity in North America that we might seek to attribute to current environmental conditions in fact originated in the ancient history of life on the continent.

The influence of past events on contemporary patterns of biodiversity has been most marked during the past 1 million years, during which climatic changes associated with glacial cycles have repeatedly disrupted the North American biota. Species ranges in North America have shifted dramatically from glacial to interglacial, and current distributions of species reflect patterns of dispersion from the most recent glacial refugia. The relative poverty of species in the more northern parts of North America in part stems from the failure of some species to disperse back into these glaciated regions in the 5000–14,000 years since the ice melted. Major climatic changes from glacial to interglacial periods also have influenced the biodiversity of unglaciated regions of the continent. For example, during the most recent glacial maximum parts of western and southwestern North America had a wetter climate. Large pluvial lakes and extensive river systems existed that are now mostly reduced to playas and dry channels. Today, desert pupfish occur only in isolated springs and pools, whereas once they were widespread in extensive lake and river systems throughout the Southwest. Once widespread palms now exist only as remnant populations in isolated canyons. In another cycle of changing climate, such remnant populations may again become common, but now we value them as rare species that enhance the biodiversity of North America. The rich and sometimes peculiar patterns of biodiversity in North America are built on a dynamic history of changing environments and changing species distributions.

In terms of the most recent history of the North American biota, the arrival of humans coincident with the end of the most recent glacial cycle is especially noteworthy. As the interglacial was beginning, hundreds of the larger animals in North America went extinct. It is difficult to account for these extinctions by changing climate alone, and it appears that human hunting pressures were a significant factor. In a brief period, the mammoths, mastadons, camels, horses, saber-tooth tigers, giant ground sloths, and many other large mammals that undoubtedly were major elements in the functioning of North American ecosystems simply disappeared from the continent. The patterns of biodiversity at the time of European settlement not many thousands of years later must reflect this fairly recent mass extinction as well as the continued influence of the few million aboriginal people who already lived in North America at that time. Whatever patterns of continental diversity we identify, we should not assume that they occurred independent of human influence.

Human influence on patterns of diversity in North America has increased greatly in the past 500 years. The European colonists consciously or inadvertently brought many new plant and animal species to this continent. Indeed, people continue to introduce species from outside North America, some of which establish
and spread to natural ecosystems well beyond the confines of urban or agricultural lands. Approximately 25% of the current flora of Canada consists of alien species; the United States has approximately 3700 alien plant species, on the order of 20% of the flora. Approximately 6% of the fishes of Canada are not native species; the United States has about 75 fish species native outside of North America and approximately 200 that have been introduced outside their native North American ranges. The fishes currently dominating the ecosystems of the Great Lakes are entirely the outcome of introduction and management of nonnative species by people. Inadvertently introduced zebra mussels are now altering ecosystem function in the Great Lakes Basin andousting native mussel species. Introduced starlings and sparrows dominate the avifauna in many settled landscapes. The landscapes and habitats of large parts of the continent have been drastically altered from pre-Columbian times. Almost all rivers in the United States have had their flow altered by dams or their drainage basin hydrology has been manipulated. Terrestrial habitats reasonably unaltered from pre-Columbian times now occupy only 48% of North America north of Mexico, and these are largely concentrated in remote mountainous or northern regions. Remnants of natural prairie and forest habitats represent only a few percent of many ecoregions in eastern North America. In western North America natural habitats are essentially obliterated in the grasslands of central California and in the interior grasslands of the Pacific Northwest. We are faced with the challenge of identifying natural patterns in the biodiversity of our native flora and fauna while the continental biota is increasingly disrupted by the introduction of alien species and the alteration of natural landscapes.

V. CONCLUSION

From the preceding discussion, assembled from a variety of sources, one point is most clear: We have really only begun to know the patterns of biodiversity in North America. The biodiversity of no group of organisms in North America is completely characterized. Some of the groups of organisms discussed in this review are reasonably well studied, but all are incompletely known. Remote parts of arctic North America are little explored and may yield new species despite the general tendency of species diversity to decrease at higher latitudes. There are unusual habitats in the high arctic that are unlike anywhere else on Earth, such as the mineral-rich hot springs on Axel Heiberg Island that emerge through hundreds of meters of permafrost. Such habitats, which are being studied as analogs for Martian polar environments, may well harbor previously unknown microbial life. The more heavily settled and biologically explored midcontinent seems well-known, but every year new localities and range extensions, and even new species, are recorded. The remote and rugged parts of southern North America undoubtedly harbor unknown species even in groups that have been well studied on the continent as a whole. Mexico is recognized as one of the top five countries in the world in terms of overall levels of biodiversity. By far the most species-rich part of North America, Mexico is ironically the least well studied.

In addition to our incomplete knowledge of species diversity in well-studied groups of organisms in North America, we must recognize that there are many other groups of organisms on the continent whose distribution and abundance are scarcely known. There are almost 91,000 species of insects described from North America north of Mexico, but this number is certainly only a small fraction of the total insect species on the continent. Almost all the insect groups are too little studied to assemble any sort of meaningful summary of their patterns of continental biodiversity. Similarly, there may be as many as 120,000 species of macrofungi in the United States alone, only one-fourth of which have been described and far fewer have been studied sufficiently to map and inventory them for the continent. The 5000–10,000 species of macrofungi (mushrooms) estimated to occur in the United States are only marginally better known. It is too early to write the definitive treatise on patterns of biodiversity in North America. There is much exciting and worthwhile work yet to do.

See Also the Following Articles

CENTRAL AMERICA, ECOSYSTEMS OF • SOUTH AMERICA, ECOSYSTEMS OF

Bibliography


