Mangroves: A Global Perspective on the Evolution and Conservation of Their Terrestrial Vertebrates

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Mangrove ecosystems are found globally along tropical and subtropical coastlines. They exhibit a steep environmental gradient between inland and marine systems, providing a unique, selective environment that shapes local morphological, physiological, and behavioral adaptations. In the first global assessment of terrestrial vertebrate species that are restricted to mangrove ecosystems, we found 48 bird, 14 reptile, 1 amphibian, and 6 mammal species endemic to mangroves, the majority of which are found in Asia and Australia. We also found that more than 40% of assessed mangrove-endemic vertebrates are globally threatened. Clearly, additional research is needed to better understand mangrove-endemic vertebrates in order to conserve them. Future research should focus on global inventories, intercontinental comparative work, and the ecology of mangrove-endemic vertebrates.

Keywords: mangrove, endemism, vertebrate, coastal ecosystem, biogeography

Mangroves are salt-tolerant, woody plants that form low-diversity forests with complex food webs and ecosystem dynamics (Macnae 1968, Tomlinson 1986). Research on mangroves has yielded many insights into their ecological functions, global patterns of floral diversity, and adaptations to saline environments, as well as into their role in fisheries—namely, as a haven for many juvenile marine species (Hogarth 2007). Nonetheless, there is practically no information about terrestrial vertebrate species in mangroves. Although terrestrial vertebrates are relatively depauperate in mangrove forests (compared with nearby tropical forests), many of the species in mangrove forests have made specific adaptations to life in the mangroves. Tropical mangrove ecosystems, like temperate salt marshes, offer a sharp environmental gradient between inland—including freshwater—and marine systems, over which selection can act and gene flow can occur (Greenberg et al. 2006). Thus, mangroves are a good system for an investigation of the forces that promote the development of local adaptation and, ultimately, the evolution of mangrove-restricted taxa.

Many factors influence the degree of local differentiation and endemism in continental habitats. Among them are selective gradients generated by abiotic stressors, the composition of source faunas in nearby habitats, the degree of isolation from source habitats, and the habitat's current extent and stability in composition, location, and historical extent (Lomolino et al. 2006). In this article, we review factors that either enhance or reduce local differentiation and endemism in terrestrial vertebrates in mangroves.

We include vertebrate species and subspecies from terrestrial environments that are found primarily in mangrove ecosystems and reproduce in them. Therefore, in this article we exclude many taxa that, although common in mangroves, do not have morphologically distinct forms that restrict them to mangrove forests. We also exclude primarily aquatic species, including fishes; marine reptiles such as crocodiles, sea turtles, and sea snakes; and marine mammals such as manatees and dolphins. We assess the extent, geographic pattern, and nature of local adaptations to mangrove conditions and discuss the conservation status of mangrove-restricted taxa in the context of environmental threats to their populations and habitat. We also mention species that depend on mangroves for only a portion of their life history (e.g., species that use mangroves only seasonally), although we do not focus on these.

Global distribution of mangroves

Mangroves are woody plants that inhabit the upper intertidal zones of saltwater areas, primarily in tropical and subtropical regions within 30° of the equator (Tomlinson 1986, Hutch-

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ings and Saenger 1987); at higher latitudes, tidal marshes replace mangroves. Mangrove vegetation covers roughly 170,000 square kilometers of the earth's surface (Spalding et al. 1997, Valiela et al. 2001), usually on soft sediments protected from extreme wave action, such as in the deltas of large rivers and estuaries and on the leeward side of barrier islands.

Analyses of species composition show that mangroves occur in two distinct biogeographical regions: the Indo–West Pacific (IWP), which includes Asia, Australia, Oceana, and the eastern coast of Africa; and the Atlantic–Caribbean–East Pacific region (ACEP), which covers the Americas and the western coast of Africa (Duke 1992). The cold water at the southern tip of Africa and the large distance between Asia and America divide the two regions. The IWP and ACEP regions have comparable total areas of mangrove habitat but very different numbers of tree genera and species (table 1). The IWP region contains more than three times as many genera, and roughly five times as many mangrove tree species, as the ACEP region does (Saenger et al. 1983, Tomlinson 1986, Ricklefs and Latham 1993). Local mangrove tree diversity in the ACEP region is generally 3 to 4 species per site, whereas the local diversity in the IWP region is 11 to 25 species per site (Macnae 1968, Chapman 1976, Bunt et al. 1991). Thus, both regional and local patterns of mangrove tree species diversity are similar, in that floral diversity in the IWP exceeds that of the ACEP. This pattern has been termed the mangrove diversity anomaly (Ricklefs and Latham 1993).

Mangrove taxa are specialized and segregated with respect to tidal height, water salinity, range of salinity of the soil, and aeration of the soil (Macnae 1968, Chapman 1976, Duke 1992). The landward fringe has the most variable floristic composition, which depends on the climate and vegetation of adjacent terrestrial habitats. In arid climates, the landward fringe can become so saline that woody plants are excluded and low-diversity salt marsh and tidal pans cover the area. However, in wet climates, the salt concentration in the landward soil is lower, and terrestrial tree species intermingle with mangrove species. Thus, wetter conditions tend to be more hospitable to a wider variety of plant species.

Table 1. Number of floral genera, floral species, and vertebrate species restricted to mangrove habitat in selected regions.

Region and subregion	Zone	Mangrove area (km^2)	Floral genera	Floral mangrove species	Vertebrate species	Amphibians	Reptiles	Birds	Mammals	Full species	Subspecies	Populations
Atlantic–Caribbean–Eastern Pacific		68,000		26								
Eastern Pacific	1	12,000	4	7	8		8		4	1	3	
West Atlantic–Caribbean	2	32,000	3	6	17	1	2	11	3	8	7	2
West Africa	3	24,000	3	5	1			1		1		
Indo–West Pacific		83,000			50							
East Africa	4	8000	8	9	1			1		1		
Indo-Malaysia	5	60,000	17	39	23		9	12	2	15	4	4
Australasia	6	15,000	16	35	26		5	20	1	14	5	7

Note: The last seven columns are included to provide extra information about the nature of endemism in each subregion.
Source: Duke (1992), modified from Ricklefs and Latham (1993). Mangrove area values are taken from FAO (2003) data.

Changes in mangrove distribution over evolutionary time

Changes in habitat availability through time can have profound effects on patterns of differentiation in taxa. Because most vertebrate differentiation in mangroves is at the subspecies level or between closely related sister species, we expect that Pleistocene events, particularly sea-level rise and changes in ocean temperatures, have had the greatest impact on evolutionary processes influencing mangrove vertebrates.

Although global patterns of mangrove tree species diversity predated the Pleistocene epoch (Ricklefs et al. 2006), Pleistocene events did affect global climate and sea levels, ultimately modifying present mangrove distributions in different regions of the world (Woodroffe and Grindrod 1991). During Pleistocene dry periods, mangrove species were more restricted than they are today to the hot, wet climate of the equator. Additionally, the drop in sea level associated with Pleistocene glacial events created broad land connections among the Malay Peninsula, Sumatra, Borneo, and Java, as well as a bridge between Australia and Papua New Guinea (Woodroffe et al. 1985, Clark and Guppy 1988, Woodroffe and Grindrod 1991), which created a large extent of suitable habitat for mangroves. Thus, while the latitudinal ranges of many mangrove species contracted during this period of maximum glaciation, newly exposed land from lower sea levels offered suitable sites for mangrove expansion along the equator. During the Pleistocene, wet climates in Southeast Asia and northern Australia, and arid climates—which are less favorable for mangrove diversity—in Africa and the New World tropics could have affected the distribution of mangrove species: patterns of aridity along American and African coasts might have contributed to range contraction of mangrove species in the ACEP, whereas increased mangrove area in Southeast Asia and Australia might have created opportunities for mangrove species expansion in the IWP.

Global and local patterns of faunal endemism

Although many vertebrate species use mangroves temporarily, relatively few terrestrial vertebrate species reside or reproduce in mangrove ecosystems. In an extensive literature search (see the online appendix at *http://nationalzoo.si.edu/ConservationAndScience/MigratoryBirds/References/default.cfm?id=45*), we detected 853 species of terrestrial vertebrates that are commonly found in mangroves, including 790 birds, 40 mammals, 20 reptiles, and 3 amphibians.

Throughout this article we use the term "mangrove restricted" to indicate mangrove endemism. Although we recognize that these species might also use other habitats on occasion, we denoted the species, subspecies, and populations in tables 2, 3, and 4 as mangrove-restricted because their life histories are tied to and dependent on mangroves. In our literature search we had to make difficult decisions between species that were restricted to mangroves but occasionally found in adjacent habitats and those species that were common both in mangroves and in adjacent habitats. When identifying species as mangrove restricted, we tried to err on the side of exclusion rather than inclusion. Given the scope of our literature search, the dearth of vertebrate faunal studies in mangroves, and the difficulty of quantitatively determining endemism to relatively small-scale linear mangrove habitats, we acknowledge that we might not have included all truly mangrove restricted species; we hope that future studies will identify any species that we have missed. We found it especially difficult to find information on reptiles in Central and South America, Africa, and Southeast Asia, and we would not be surprised if over time more mangrove-endemic reptile species are identified. However, we used the best available knowledge, and we are confident that the vast majority of mangrove-endemic species are on our list. Only future field studies on vertebrates in mangroves and adjacent habitat types will be able to determine whether more species are endemic to mangrove ecosystems. We see this article as a starting point that we hope will inspire further research on vertebrates in mangrove ecosystems.

From our literature search, we identified 69 terrestrial vertebrate species (39 species, 16 subspecies, and 14 distinct

Table 2. Distribution and conservation status of vertebrate amphibian and reptile taxa restricted to mangroves.

Species	Subspecies	Taxonomic level of restriction	Distribution (region of mangrove)	IUCN status
Mangrove frog (*Eleutherodactylus caribe*)	–	Species	Haiti	CR
Mangrove terrapin (*Malaclemys terrapin*)	*rhizophorarum*	Subspecies	Southern Florida and Keys, North America	NT
Water monitor (*Varanus salvator*)	*cumingi, marmoratus*	Subspecies	Philippine Islands	–
Mangrove monitor (*Varanus indicus*)	–	Species	Papua New Guinea and Australia	–
Little file snake (*Acrochordus granulatus*)	–	Species	India to Australia	–
Mangrove snake (*Boiga dendrophila*)	–	Species	Southeast Asia to the Philippines	–
Yellow-banded water snake (*Cantoria violacea*)	–	Species	Andaman Islands	–
Dog-faced water snake (*Cerberus rynchops*)	–	Species	India to Southeast Asia	–
Australian bockdam (*Cerberus australis*)	–	Species	Northern Australia	–
Crab-eating snake (*Fordonia leucobalin*)	–	Species	India to Australia	–
Glossy marsh snake (*Gerarda prevostiana*)	–	Species	India to Thailand	–
Red-tailed green rat snake (*Gonyosoma oxycephala*)	–	Species	Southeast Asia to the Philippines	–
Richardson's mangrove snake (*Myron richardsonii*)	–	Species	Northern Australia	–
Mangrove water snake (*Nerodia clarkii*)	*compressicauda*	Subspecies	Southern Florida, North America	LC
Mangrove pit-viper (*Trimeresurus purpureomaculatus*)	*andersonii and purpureomaculatus*	Subspecies	India to Singapore	–

Note: Status refers to the IUCN Red List global status for each species: CR, critically endangered; DD, data deficient; EN, endangered; LC, least concern; NT, near threatened; and VU = vulnerable. An en dash in the column under IUCN status indicates that the global status of this species has not been assessed. We include geographically restricted populations in this table because they warrant future investigation for possible divergence from parent populations.

populations) that either are restricted to mangroves or have recognized subspecies or populations restricted primarily to mangroves. In our summary of these data, we refer to the aforementioned mangrove-restricted populations and subspecies as "species," because they are distinct species in relation to the other species that are mangrove endemic. One amphibian, 14 reptile (table 2), 48 bird (table 3), and 6 mammal species or subspecies (table 4) are restricted to mangroves. These species are from a wide variety of vertebrate lineages, including frogs, turtles, lizards, snakes, hummingbirds, egrets, rails, kingfishers, hawks, woodpeckers, passerines, bats, monkeys, sloths, and rodents. We found an additional 18 bird and 2 mammal species that are dependent on mangroves for feeding, roosting, or nesting during daily or seasonal migrations, but that are not considered restricted to mangroves overall (table 5). In a similar literature search, 25 terrestrial vertebrate species were determined to be endemic to (or to have subspecies restricted primarily to) tidal marshes, including turtles, snakes, emberizid sparrows, rails, shrews, and small rodents (Greenberg et al. 2006).

Geographic distributions of faunal endemics

The majority of the listed mangrove-restricted species (or species with at least one mangrove-restricted subspecies) are located in Asia and northern Australia. Australia and Asia have the most mangrove-restricted species, 26 and 23 species, respectively, followed by the West Atlantic and Caribbean (17 species), the Pacific coast of the Americas (8 species), and western and eastern Africa (1 species each) (table 1, figure 1). Thus, the IWP region has almost twice the number of mangrove-restricted terrestrial vertebrate species (50 species) as the ACEP region (26 species). Mangrove-restricted birds, mammals, amphibians, and reptiles are found in Asia, Australia, and North America, whereas only birds are restricted to mangroves in South America and Africa.

Previous research suggests that although there are similar numbers of bird species found in mangroves throughout the world, the highest numbers of mangrove-restricted bird species are found in Australia and Southeast Asia. Altenburg and Spanje (1989) detected 125 bird species in the mangroves of Guinea-Bissau in West Africa, but most of these species used mangroves only for roosting. Only one species, a nectivorous sunbird (*Anthreptes gabonicus*) was confined to mangroves (Cawkell 1964, Field 1968). In the Neotropics, Haverschmidt (1965) and Ffrench (1966) listed 84 and 94 species that use mangroves in Suriname and Trinidad, respectively, but in both countries, only one species, a crab-eating hawk (*Buteogallus aequinoctialis*), was reported to be restricted to mangroves. In peninsular Malaysia, Nisbet listed 125 bird species in mangroves, 7 of which were restricted to mangroves (Nisbet 1968, Medway and Wells 1976). The results from these studies correspond with our finding that Southeast Asia and Australia have more mangrove-restricted species than other regions.

Other taxa also show greater mangrove-associated diversity in the IWP than in the ACEP region. In addition to terrestrial vertebrate diversity, the diversity of flora, crabs, and mollusks in mangroves are all greater in the IWP region (Saenger et al. 1983, Ricklefs and Latham 1993), indicating a strong correlation between mangrove tree diversity and associated animal diversity, which is consistent with other terrestrial environments (Qian and Ricklefs 2008).

Potential causes of mangrove specialization

The majority of mangrove-restricted species (49 species) have sister taxa in terrestrial habitat, whereas a smaller number of species (20) have close taxonomic relationships with taxa living in freshwater wetlands. In this section we focus on the species with terrestrial origins. Two potential factors might explain why species and populations that were formerly associated with terrestrial habitat currently have mangrove-restricted ranges: (1) the exclusion of species from nearby habitat through biotic competition, and (2) the use of mangroves as refugia during climate change events, such as those that dried out adjacent habitat. Subsequent specialization to mangroves most likely occurred in at least two ways:

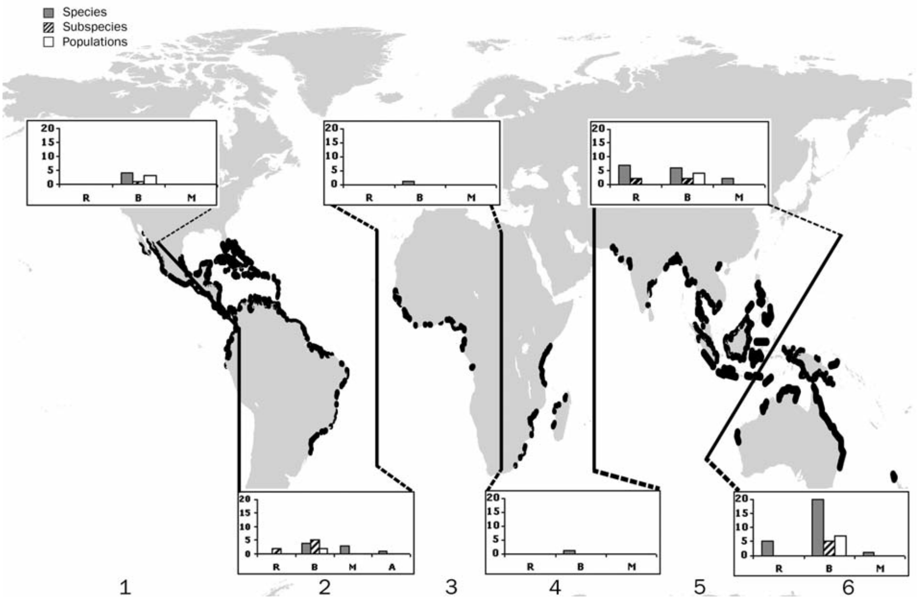

Figure 1 Global distribution of mangroves divided into six biogeographical regions (see table 1). Graphs indicate the number of mangrove-restricted species in different categories of local differentiation in each biogeographical region. Abbreviations: A, amphibian; B, birds; M, mammals; R, reptiles. Global mangrove distribution is modified from Chapman (1976) and WWF Global 200 (Olson DM and Dinerstein 2006).

Table 3. Distribution and conservation status of bird taxa restricted to mangroves.

Species	Subspecies	Taxonomic level of restriction)	Distribution (region of mangrove)	IUCN status
Striated heron (*Butroides striatus*)	*stagnatilis*	Subspecies	Northern Australia	LC
Great-billed heron (*Ardea sumatrana*)	–	Population	Papua New Guinea and Australia (Kimberley, Western Australia)	LC
Reddish egret (*Egretta rufescens*)	–	Species	Florida, Caribbean and Central America	LC
Madagascar Teal (*Anas bernieri*)	–	Species	Madagascar	EN
Rufous crab-hawk (*Buteogallus aequinoctialis*)	–	Species	Venezuela to Brazil	LC
Common black-hawk (*Buteogallus anthracinus*)	*gundlachii*	Subspecies	Cuba	LC
Mangrove black-hawk (*Buteogallus subtilis*)	–	Species	Pacific Coast of Central America	LC
Grey-necked wood-rail (*Aramides cajanea*)	*avicenniae*	Subspecies	São Paulo to Santa Catarina, Brazil	LC
Rufous-necked wood-rail (*Aramides axillaris*)	–	Population	Central and South America (Central America)	LC
Chestnut rail (*Eulabeornis castaneoventris*)	–	Species	Papua New Guinea and Australia	LC
Plain-flanked rail (*Rallus wetmorei*)	–	Species	Venezuela	EN
Clapper rail (*Rallus longirostris*)	11 tropical subspecies	Subspecies	Central and South America	LC
Mangrove hummingbird (*Amazilia boucardi*)	–	Species	Pacific Coast of Costa Rica	EN
Saphire-bellied hummingbird (*Lepidopyga lilliae*)	–	Species	Colombia	CR
Brown-winged kingfisher (*Pelargopsis amauroptera*)	–	Species	East India to Malaysia	LC
Ruddy kingfisher (*Todiramphus coromanda*)	Minor	Subspecies	Thailand to Borneo (Malaysia)	NT
Collared kingfisher (*Todiramphus chloris*)	–	Subspecies	Australia	LC
Greater flameback (*Chrysocolaptes lucidus*)	*chersonesus, andrewsi, strictus, kangeanensis*	Subspecies	India to Southeast Asia (Malaysia to Bali)	LC
Laced woodpecker (*Picus vittatus*)	–	Population	Thailand to Indonesia (Western Thailand)	LC
Mangrove pitta (*Pitta megarhyncha*)	–	Species	India to Southeast Asia	NT
Straight-billed woodcreeper (*Xiphorhynchus picus*)	*extimus*	Population	Central and South America (western coast of Central America)	LC
Mangrove blue flycatcher (*Cyornis rufigastra*)	–	Species	Thailand to Papua New Guinea (everywhere except Sulawasia)	LC
Magpie robin (*Copsychus saularis*)	–	Population	India to Singapore (Malaysia)	LC
Mangrove grey fantail (*Rhipidura phasiana*)	–	Population	Papua New Guinea and Australia (northern Australia)	LC
Rufous fantail (*Rhipidura rufifrons*)	*dryas*	Population	Australia (Kimberley, western Australia, and West Queensland)	LC
Shiny flycatcher (*Myagra alceto*)	–	Population	Australia (Kimberley, western Australia, and West Queensland)	LC
Broad-billed flycatcher (*Myiagra ruficollis*)	–	Population	Papua New Guinea and Australia (West Queensland)	LC
Mangrove whistler (*Pachycephala grisola*)	–	Species	India to Southeast Asia	LC
White-breasted whistler (*Pachycephala lanioides*)	–	Species	Australia	LC
Mangrove golden whistler (*Pachycephala melanura*)	*robusta*	Subspecies	Papua New Guinea and Australia (Northern Territory, Australia)	LC
Ashy tailorbird (*Orthotomus ruficeps*)	*ruficeps*	Population	Indonesia (Java)	LC
Mangrove gerygone (*Gerygone levigaster*)	–	Species	Papua New Guinea and Australia	LC
Dusky gerygone (*Gerygone tenebrosa*)	–	Species	Western Australia	LC
Large-billed gerygone (*Gerygone magnirostris*)	*magnirostris*	Subspecies	Papua New Guinea and Australia (Kimberley, western Australia)	LC
Great tit (*Parus major*)	*ambiguous*	Population	Europe to Asia (Malaysia)	LC
Mouse-brown sunbird (*Anthreptes gabonicus*)	–	Species	Western Africa	LC
Copper-throated sunbird (*Nectarinia calcostetha*)	–	Species	Thailand to Papua New Guinea (Malaysia to Bali)	LC
Red-headed myzomela (*Myzomela erythrocephala*)	–	Species	Papua New Guinea and Australia	LC

(continued)

Table 3. (continued)

Species	Subspecies	Taxonomic level of restriction	Distribution (region of mangrove)	IUCN status
Yellow whiteeye (*Zosterops lutea*)	–	Species	Australia	LC
Mangrove honeyeater (*Lichenostomus fasciogularis*)	–	Species	Papua New Guinea and Australia	LC
Varied honeyeater (*Lichenostomus versicolor*)	–	Population	Papua New Guinea and Australia (Northwestern Queensland, Australia)	LC
Mangrove vireo (*Vireo pallens*)	–	Population	Central America and the Caribbean (Pacific Coast of Mexico)	LC
Prairie warbler (*Dendroica discolor*)	*paludicola*	Subspecies	Southern Florida, North America	LC
Yellow “mangrove” warbler (Dendroica petechia)	34 subspecies	Subspecies	Central America and the Caribbean	LC
Lemon-breasted flycatcher (*Microeca flavigaster*)	*tormenti*	Subspecies	Australia (Kimberley, western Australia)	LC
Mangrove robin (*Eopsaltria pulverulaenta*)	–	Species	Australia	LC
Black butcherbird (*Cracticus quoyi*)	–	Population	Australia (Northern Territory, Australia)	LC
Mangrove finch (*Camarhynchus heliobates*)	–	Species	Galápagos Islands, Ecuador	CR

Note: Status refers to the IUCN Red List global status for each species: CR, critically endangered; DD, data deficient; EN, endangered; LC, least concern; NT, near threatened; and VU, vulnerable. We include geographically restricted populations in this table because they warrant future investigation for possible divergence from parent populations.

through dependence on the structure and microclimate of mangroves (especially true when adjacent inland habitat is arid), and through specialization on particular kinds of food not found in other closed-canopy habitats, such as crabs and certain types of nectar.

In many cases, specialization to mangrove habitat was probably achieved during arid Pleistocene periods when wet forests contracted or disappeared in many places. During these arid cycles mangroves would have acted as refuges for closed-canopy species. For example, Ford (1982) and Schodde and colleagues (1982) posited that as Australia dried out during Pleistocene glacial periods (Longmore and Hiejnis 1999), northwestern Australian rainforests contracted and fragmented into patches too small to support viable populations of many bird species, while eastern Australian rainforest patches were relatively larger and retained more species (Nix and Kalma 1972). It has been further hypothesized that many isolated taxa then adapted to mangrove habitat in northwestern Australia, possibly because it was the only closed habitat available, and its climatic buffering ensured more stable food sources (Ford 1982, Schodde et al. 1982). Meanwhile, the interchange of species between mangroves and rainforest might have limited the emergence of mangrove specialists. As a likely result of these historical events, fewer bird species are specialized on the mangroves in eastern Australia (8 subspecies), where mangroves are contiguous with rainforest, than in northwestern Australia (9 species and 14 subspecies), where the inland habitat is arid and lacks rainforest (Ford 1982).

Searching the available literature, we found a similar pattern in Central America. The Pacific coast of Central America, which is drier than the Atlantic coast, appears to have more bird species restricted to mangroves (6 species) than does the Atlantic coast (3 species), though field investigations of mangrove-restricted species in Central America have not been conducted to confirm this observation. It seems that mangrove specialists might be more likely to arise in areas of geographical isolation, which could prevent gene flow between a potential specialist and its parent species.

Mangroves provide food sources not available in inland habitat. Of the 69 mangrove-restricted species, 15 species eat mainly crabs and 7 feed predominantly on nectar from mangrove trees. Thus, 32% of mangrove-restricted terrestrial vertebrate species feed primarily on food sources that are unavailable in adjacent inland habitat. The majority of the ground-foraging species eat primarily crabs, which constitute a large amount of the biomass found in mangroves (Jones 1984), whereas species foraging in other forest strata eat a variety of foods that are potentially available in other habitats as well, such as insects and small vertebrates. Ground-foraging species therefore seem most likely to depend on mangrove-specific food.

Adaptations to mangrove life

Terrestrial species living in mangroves face a number of environmental challenges not usually present in inland habitat, such as regular tidal inundation and less-predictable storm surges, anaerobic soil conditions, and a saline environment. It is well known that mangrove plants have developed a variety of adaptations to deal with salt stress and anoxic soils, including salt exclusion from their roots, salt excretion from their leaves, and aerial roots (Ball 1996), but adaptations of vertebrate species to conditions in mangroves are poorly documented.

All terrestrial vertebrates face similar problems of salt accumulation and water loss in saltwater. Reptiles, turtles,

Table 4. Distribution and conservation status of vertebrate mammal taxa restricted to mangroves.

Species	Taxonomic level of restriction	Distribution (region of mangrove)	IUCN status
Pygmy three-toed sloth (*Bradypus pygmaeus*)	Species	Bocas del Toro, Panama	CR
Vordermann's Pipistrelle (*Pipistrellus vordermanni*)	Species	Borneo	DD
Northern pipistrelle (*Pipistrellus westralis*)	Species	Northern Australia	LC
Proboscis monkey (*Nasalis larvatus*)	Species	Borneo	EN
Garrido's hutia (*Mysateles garridoi*)	Species	Cuba	CR
Cabrera's hutia (*Mesocapromys angelcabrerai*)	Species	Cuba	CR

Note: Status refers to the IUCN Red List global status for each species: CR, critically endangered; DD, data deficient; EN, endangered; LC, least concern; NT, near threatened; and VU, vulnerable. We include geographically restricted populations in this table because they warrant future investigation for possible divergence from parent populations.

lizards, and sea snakes developed postorbital glands, nasal glands, and sublingual glands, respectively, to handle salt stress (Dunson 1975). For example, specialized nasal glands have been identified in rails (Olson S 1997). For rail species with both salt and freshwater populations, the nasal glands are larger in the saltwater populations. The difference has been shown to have both a genetic and a developmental basis in clapper rails (*Rallus longirostris*), a species that has mangrove-specialist subspecies (Olson S 1997).

The mangrove-restricted dog-faced water snake (*Cerberus rynchops*) has a small premaxillary salt gland to excrete saltwater. Its rate of salt excretion is low compared with that of marine reptiles, but still allows *C. rynchops* to survive for long periods in seawater (Dunson and Dunson 1979). The skin of *C. rynchops* exhibits a low rate of cutaneous oxygen exchange and a low rate of dermal water exchange, which might help explain its ability to live in saltwater with a small and relatively low-output salt gland. The ability of *C. rynchops* to tolerate salt and freshwater facilitates its survival in mangrove ecosystems. Whether other mangrove-restricted prey, such as insects, nectar, and crabs, provide salt-balance challenges for mangrove-restricted predators remains to be investigated.

Morphological differences from inland relatives

Because little has been written about the morphology of mangrove-restricted terrestrial vertebrates, there is scant information on adaptations or morphological differences between mangrove-restricted and inland populations. In our literature search, we found that a majority of mangrove-restricted terrestrial reptiles tend to have laterally compressed tails, which are presumed to be helpful in aquatic environments. Most mangrove-restricted snakes are defined by a suite of adaptations for aquatic life, such as valvular nostrils, dorsally oriented eyes, a glottis that can be extended to fit into the internal nares, and a shallowly notched rostral that permits tight closure of the mouth (Gyi 1970). Our analysis found that mangrove-restricted terrestrial snakes tend to have dark-gray to olive-brown coloration, whereas arboreal mangrove-restricted snakes do not seem to exhibit any coloration pattern.

The most striking morphological difference between mangrove-dependent vertebrates and their close relatives in adjacent inland forest is that many bird species in mangroves tend to have longer and narrower bills. We found that 21% of birds restricted to mangroves, excluding hawks and waterbirds, have bills larger than those of related subspecies or sister species inhabiting inland habitat. Mangrove bird species with larger bills comprise both arboreal and ground foragers that feed primarily on crabs or insects, and larger bills are most prominent among passerine species that feed primarily on the ground. Three out of four ground-foraging, mangrove-restricted passerine species have larger bills than do their closest inland relatives. In a study similar to ours, Grenier and Greenberg (2005) found that sparrows restricted to tidal marshes also have bills that are larger than those of close relatives that are nontidal. In addition, Ricklefs (2004) found that birds on islands have greater bill length than do mainland relatives. The significance of larger bills is not well understood, but could be related to reliance on different or larger food items or wider foraging niches in tidal systems and islands.

Life history of mangrove vertebrates

Mangrove-restricted reptiles and mammals feed on a variety of food sources that are specific to mangrove habitat. Ground snakes tend to search mud flats, tree roots, and tidal channels for crabs, shrimp, and fish. In contrast to ground snakes, arboreal snakes usually feed on birds, mammals, and lizards. Crabs also form a large part of the diet of mangrove-restricted lizards, which are otherwise omnivorous and have a highly opportunistic diet (Pianka and King 2004). Of the six mammal species restricted to mangroves, four eat primarily leaves and two are insectivorous bats.

Our study found that 51% of mangrove-restricted bird species feed primarily on insects, followed by smaller proportions that feed on crabs (27%), nectar (16%), and fish (4%). More specifically, mangrove-restricted bird species feed primarily on insects in the canopy (35%), on muddy substrate (34%), in water (15%), and on trunks and limbs of trees (3%); 11% feed on nectar, and 2% are strictly aerial insectivores. Our results are supported by three studies that looked at the feeding habits of all avian species detected in mangroves.

Table 5. Species that are not restricted to mangroves but nonetheless depend on mangrove habitat for food, nesting, or during seasonal migration.

Species	Subspecies	Distribution (region of mangrove restriction)	Mangrove use	IUCN status
Brahminy kite (*Haliastur indus*)	–	India to Australia (Australia)	Nest	LC
Willet (*Catoptrophorus semi-palmatus*)	–	North and South America	Seasonal migrant, roost	LC
Whimbrel (*Numenius phaepus*)	–	Global	Seasonal migrant, roost	LC
Terek sandpiper (*Tringa terek*)	–	Asia and Australia	Seasonal migrant, roost	LC
White-crowned pigeon (*Columba leucocephala*)	–	Caribbean and Central America (Florida and Costa Rica)	Daily migrant, nest	LC
Pied imperial-pigeon (*Ducula bicolor*)	*bicolor*	Malaysia and Indonesia	Seasonal migrant, nest	LC
Mountain imperial-pigeon (*Ducula badia*)	*badia*	Malaysia and Indonesia	Seasonal migrant, roost	LC
Pink-necked green-pigeon (*Treron vernans*)	–	Malaysia	Seasonal migrant, roost	LC
Yellow vented green-pigeon (*Treron seimundi*)	*seimundi*	Malaysia	Seasonal migrant, roost	LC
Island collared-dove (*Streptopelia bitorquata*)	–	Indonesia and Philippines	Daily migrant, roost	LC
Zenaida dove (*Zenaida aurita*)	*salvadorii*	Yucatan Peninsula and the Caribbean (Yucatan Peninsula)	Daily migrant, roost	LC
Philippine cockatoo (*Cacatua Haematuropygia*)	–	Philippine Islands	Dependent because of loss of primary habitat	CR
Mangrove cuckoo (*Coccyzus minor*)	*maynardii*	Florida	Seasonal migrant, nest	LC
African mangrove kingfisher (*Halcyon senegaloides*)	–	East Africa	Seasonal migrant	LC
Yellow-billed cotinga (*Carpodectes antoniae*)	–	Pacific Coast of Costa Rica and Panama	Seasonal migrant, nest	EN
Prothonotary warbler (*Protonotaria citrea*)	–	Central and northern South America	Seasonal migrant	LC
Northern waterthrush (*Seiurus novaboracensis*)	–	Central and northern South America	Seasonal migrant	LC
Yellow-shouldered blackbird (*Agelaius xanthomus*)	–	Puerto Rico	Dependent because of loss of primary habitat	EN
Little north-western freetail bat (*Mormopterus loriae*)	*cobourgensis*	Northwestern Australia	Daily migrant, roost	LC
False water rat (*Xeromys myoides*)	–	Australia	Daily migrant, feed	VU

Note: Status refers to the IUCN Red List global status for each species: CR, critically endangered; DD, data deficient; EN, = endangered; LC, least concern; NT, near threatened; and VU, vulnerable. We include geographically restricted populations in this table because they warrant future investigation for possible divergence from parent populations.

Noske (1995, 1996), who studied foraging guilds in Malaysia and northern Australia, found that in Malaysia, the largest guild in both locations was foliage insectivores, followed by nectarivores, bark forages, and ground foragers; in northern Australia, ground foragers and nectarivores were the largest guilds. In Central America, Lefebvre and Poulin (1997) found a majority of foliage insectivores, followed by bark foragers.

Pantropical studies of avian foraging guilds in lowland humid forests also found that foliage insectivores make up the largest foraging guild, with frugivores and bark foragers the second and third most common foraging guilds (Pearson 1977, Karr 1980). Frugivores and granivores are noticeably absent from our list of mangrove-restricted species, presumably because there are few food sources for them in the mangroves. However, both frugivores and granivores have often been observed using mangrove habitat to nest and roost while foraging in adjacent inland habitat.

Some bird species exhibit a zonal pattern that corresponds with that of mangrove tree species (Noske 1995, 1996). In some cases, potentially competing species occupy largely mutually exclusive zones such as the seaward fringe, tidal channel, saline flats, or landward fringe. Such zonation has been observed in woodpeckers in Malaysia (Noske 1995), and in gerygones (Noske 1996) and kingfishers (Schodde et al. 1982) in Australia. The structure of the foliage and branching patterns between different mangrove tree species seems to differ enough that in the presence of competitors, birds can specialize on different mangrove tree species. Noske (1996) reported that in Australia the correspondence between plant and bird zonation was stronger in the dry season than in the wet season, possibly because of restricted insect abundance during the dry season. Presumably zonation between species in the same feeding guilds occurs in an effort to avoid direct competition for food resources.

Threats to mangrove diversity

Throughout their range, mangroves and their associated biota are threatened by human activities such as mangrove destruction and overexploitation, as well as by more indirect anthropogenic factors such as pollution and climate change. In the period 1980–2001, the world lost between 19% and 35% of its total mangrove forest area (Valiela et al. 2001, FAO 2003). On average, 3000 square kilometers of mangrove forest were lost each year between the early 1980s and 2001, which is about 2.1% per year. At this rate of loss, mangroves could be extinct in 100 years (Duke et al. 2007). Mangroves are already critically endangered or approaching extinction in 26 of the 120 countries in which they exist (FAO 2003). Growing pressures from urban and industrial development along coastlines, combined with climate change and sea-level rise, make the need to conserve, protect, and restore tidal wetlands increasingly urgent (Barbier 2007). If the destruction of mangroves continues, these forests might be reduced to relic patches too small to support the diversity of organisms that depend on them.

Conservation status of mangrove faunal species

Our study examined the threat status of mangrove-restricted terrestrial vertebrate species using the IUCN Red List to assess threat. For the most part, the IUCN Red List (IUCN 2007) includes only full species. Thus, the level of threat for the 16 subspecies and 14 populations that are mangrove restricted has not been investigated. In addition, the 12 species of old-world reptiles that are mangrove restricted have not yet been evaluated by the IUCN. Of the remaining 27 mangrove-restricted species that have been assessed, 13 are listed as threatened (tables 2, 3, 4). Eleven of the 13 threatened species have restricted ranges and the major known threat to their survival is habitat destruction (IUCN 2007). Given the current rate of mangrove destruction and our lack of knowledge about the population densities and life histories of terrestrial vertebrates in mangroves, research on these organisms is desperately needed to prevent the mangroves and their associated fauna from disappearing entirely.

Mangroves also provide a last refuge for species that have lost their original habitat (Ellison 2004). A few examples are the yellow-shouldered blackbird (*Agelaius xanthomus*) and the Philippine cockatoo (*Cacatua haematuropygia*). While the primary habitat for these species had been inland forests, they are currently restricted to mangroves, and presumably could have gone extinct had they not been able to use mangroves as a last refuge.

Future research needs

An abundance of research is needed to better understand mangrove species and to better direct conservation initiatives to conserve them. A good place to start would be to examine why endemism for mangrove species and subspecies in Southeast Asia and Australia is higher than endemism for the rest of the world. Several factors could explain the difference in vertebrate diversity between the IWP and ACEP biogeographical regions, including present-day species-area relationships, historical species-area relationships (see the section on changes in mangrove distribution over evolutionary time), differences in floral diversity (which provide a greater diversity of resources), and a geographic bias in sampling efforts. The difference in faunal diversity among the regions does not seem to be dependent on the current amount of available mangrove habitat, as mangroves today cover roughly the same amount of area in the IWP as in the ACEP (see table 1). Although present mangrove floral diversity has a strong correlation with diversity of mangrove-restricted terrestrial vertebrates, no studies corroborate this hypothesis. If this higher endemism results partly from biases in the way that subspecies are recognized and described, then a more globally standardized approach to research on the differentiation of mangrove taxa will provide a more complete inventory of mangrove-restricted taxa. Additionally, researchers should coordinate investigations at sites on multiple continents to determine whether the regional patterns of endemism reported in this article are also represented at the local scale. These investigations might also give insight into global causes of endemism.

Another interesting field of investigation would be to determine which mangrove-restricted species are evolutionarily adapted to mangroves, and which species are competitively excluded from adjacent inland habitat. Additionally, surveys for cryptic microgeographic variation in mangrove species might determine that there are more mangrove specialists than are now known. Finally, researchers might study genetic divergence between individuals with both inland and mangrove populations to determine the degree of divergence between populations, and to develop estimates of minimum coalescence times for mangrove populations to become distinct from inland populations in different regions. In addition, mangroves are an ideal place to investigate many fundamental ecological principles, such as ecological release, species packing, and density compensation.

Given the threats to mangrove ecosystems, researchers should expand both modeling and empirical monitoring approaches to determine how the distribution of different species will respond to regional habitat loss, fragmentation, and changes to hydrology from sea-level changes and modifications from inland sources. The IUCN is currently completing its Red List for all mangrove plant species, and future research should tie together the mangrove plant and animal Red List species. In addition, researchers should identify mangrove sites that are particularly important to resident vertebrate species and wintering populations of migratory birds. As a result of hydrology and the slope of the continental shelf, some sites will have better food resources than others (Lefebvre and Poulin 1997).

Conclusions

Many terrestrial vertebrate species have differentiated at the species or subspecies level in response to the sharp environmental gradient between mangroves and inland habitat. Characteristics associated with species and subspecies specific to mangroves include differences in the coloration of birds and in the size and shape of their beaks. The majority of mangrove-restricted species are in Southeast Asia and Australia.

Although there is no single, comprehensive explanation for this biogeographical phenomenon, historical species-area relationships, differences in floral diversity, and a geographic bias in sampling effort provide plausible causes.

Mangroves are threatened by development, pollution, mariculture, and changes in sea level and salinity. The global impact of such threats on mangrove taxa remains poorly understood, as mangrove ecology and conservation are usually approached at a local rather than a global scale. A global approach to research on mangrove taxa can provide a more complete view of the factors responsible for the observed patterns of differentiation, and will be useful to future efforts to conserve mangrove forests.

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