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DIVERSITY AND ENDEMISM IN TIDAL-MARSH VERTEBRATES

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Abstract. Tidal marshes are distributed patchily, predominantly along the mid- to high-latitude coasts of the major continents. The greatest extensions of non-arctic tidal marshes are found along the Atlantic and Gulf coasts of North America, but local concentrations can be found in Great Britain, northern Europe, northern Japan, northern China, and northern Korea, Argentina-Uruguay-Brazil, Australia, and New Zealand. We tallied the number of terrestrial vertebrate species that regularly occupy tidal marshes in each of these regions, as well as species or subspecies that are largely restricted to tidal marshes. In each of the major coastal areas we found 8–21 species of breeding birds and 13–25 species of terrestrial mammals. The diversity of tidal-marsh birds and mammals is highly inter-correlated, as is the diversity of species restricted to saltmarshes. These values are, in turn, correlated with tidal-marsh area along a coastline. We estimate approximately seven species of turtles occur in brackish or saltmarshes worldwide, but only one species is endemic and it is found in eastern North America. A large number of frogs and snakes occur opportunistically in tidal marshes, primarily in southeastern United States, particularly Florida. Three endemic snake taxa are restricted to tidal marshes of eastern North America as well. Overall, only in North America were we able to find documentation for multiple taxa of terrestrial vertebrates associated with tidal marshes. These include one species of mammal and two species of birds, one species of snake, and one species of turtle. However, an additional 11 species of birds, seven species of mammals, and at least one snake have morphologically distinct subspecies associated with tidal marshes. Not surprisingly, species not restricted entirely to tidal marshes are shared predominantly with freshwater marshes and to a lesser degree with grasslands. The prevalence of endemic subspecies in North American marshes can either be a real biogeographical phenomenon or be attributable to how finely species are divided into subspecies in different regions. The difference between North America and Eurasia is almost certainly a biological reality. Additional taxonomic and ecological work needs to be undertaken on South American marsh vertebrates to confirm the lack of endemism and specialization there. Assuming that the pattern of greater degree of differentiation in North American tidal-marsh vertebrates is accurate, we propose that the extension and stability of North American marshes and the existence of connected southern refugia along the Gulf Coast during the Pleistocene contributed to the diversification there. The relatively large number of endemics found along the west coast of North America seems anomalous considering the overall low diversity of tidal marsh species and the limited areas of marsh which are mostly concentrated around the San Francisco Bay area.

Key Words: biogeography, habitat specialization, saltmarsh, wetland vertebrates.

DIVERSIDAD Y ENDEMISMO EN VERTEBRADOS DE MARISMA DE MAREA

Resumen. Los marismas de marea se distribuyen en parches, predominantemente por las costas de media-a alta latitud de los grandes continentes. Las extensiones mayores de marismas de marea no-árticos son encontradas a lo largo de las costas del Atlántico y del Golfo de Norte América, pero concentraciones locales pueden ser encontradas en Gran Bretaña, el norte de Europa, el norte de Japón, el norte de China y el norte de Corea, Argentina-Uruguay-Brasil, Australia y Nueva Zelanda. Enumeramos el numero de especies de vertebrados terrestres que regularmente ocupan las marismas de marea en cada una de estas regiones, así como especies o subespecies que son ampliamente restringidas a marismas de marea. En cada una de las áreas costeras principales encontramos 8–21 especies de aves reproductoras y 13–25 especies de mamíferos terrestres. La diversidad de aves y mamíferos de marismas de marea se encuentra altamente inter-correlacionada, así como la diversidad de especies restringidas a marismas saladas. Estos valores son por lo tanto, correlacionados con el área marisma-marea a lo largo de la línea costera. Estimamos que aproximadamente siete especies de tortugas aparecen en aguas salobres o marismas saladas en todo el mundo, pero solo una especie es endémica, y es encontrada en el este de Norte América. Un gran numero de ranas y culebras aparecen oportunísticamente en marismas de marea, principalmente en el sureste de Estados Unidos, particularmente en Florida. Tres taxa de culebras endémicas son restringidas a marismas de marea también del este de Norte América. Sobre todo, solo en Norte América fuimos capaces de encontrar documentación de múltiples taxa de vertebrados terrestres asociados a marismas de marea. Esto incluye una especie de mamífero y dos especies de aves, una especie de culebra y una de tortuga. Sin embargo, 11 especies adicionales de aves, siete de mamíferos, y al menos una culebra, tienen subspecies que son morfológicamente distintas y que estan asociadas con marismas de marea. No es de sorprenderse, pero las especies no son restringidas completamente a marismas de marea son compartidas predominantemente con marismas de agua fresca y no a menor grado con pastizales. El predominio de subespecies endémicas en marismas de Norte América se debe ya sea a un fenómeno biogeográfico real, o puede ser atribuido a que especies son divididas finamente en subespecies en diferentes regiones. La diferencia entre Norte América y Eurasia es casi ciertamente una realidad biológica. Trabajo taxonómico y ecológico adicional debe de ser llevado a cabo en vertebrados de marisma en Sudamérica para confirmar la falta de endemismo y especialización ahí. Asumiendo que el patrón de mayor grado de diferenciación de vertebrados de marisma en Norte América es correcto, proponemos que la extensión y la estabilidad de marismas en Norte América, y la existencia de refugios sureños conectados a lo largo de la costa del Golfo durante el Pleistoceno, contribuyó a la diversificación ahí. El relativamente gran número de endemismos encontrados a lo largo de la costa oeste de Norte América, parece anormal considerando el total de diversidad baja de especies de marismas de marea y las áreas limitadas de marisma, las cuales están principalmente concentradas alrededor del área de la bahía de San Francisco.

Tidal marshes associated with well-protected shorelines of low relief at mid- to high latitudes, are found at the margins of all major continents except Antarctica (Chapman 1977). Along with tropical and subtropical mangrove swamps, tidal marshes are a true ecotone between marine and terrestrial systems, and as such present a number of adaptive challenges to vertebrate species. Perhaps the most obvious and critical feature of tidal marshes is salinity, with salt concentration ranging from zero parts per thousand (ppt) to concentrations >35 ppt. The regular influx of tidal waters causes water levels to be variable and in the intertidal zone creates regular fluctuations between flooded and exposed muddy substrates. Tidal levels vary throughout the year and in conjunction with storm systems can cause both seasonal and unpredictable flooding. Saltmarshes are dominated by a few species of salt-tolerant (halophytic) plants. Where the dominant plants are grasses and shrubs, the above-ground strata of the marsh come to resemble freshwater marshes and grasslands. In more arid regions, lower portions of tidal marsh are dominated by other halophytic plants, such as *Salicornia* spp. that render the marshes structurally quite distinct from most interior habitats. Species diversity of plants increases with latitude (up to a point) and decreases with salinity (Chapman 1977).

Marine invertebrates, such as amphipods, decapods, and gastropods, dominate the fauna of the muddy substrate of tidal marshes (Daiber 1982). The low species diversity of plants, their high reliance on vegetative means of reproduction, and the regular washing of the substrate by tidal waters decrease the availability of seeds and fruits to saltmarsh vertebrates. These adaptive challenges, and others, combine to form a selective environment that should lead to local adaptive modifications of terrestrial vertebrates colonizing the marshes. However, several biogeographical features may act to reduce the ability of genetically based divergence to evolve in local tidal marsh populations. Overall, tidal marshes are limited in extent and with the exception of a few large estuarine systems, e.g., San Francisco and Chesapeake bays in North America, and the estuary of the Rio de la Plata in South America, tidal marshes are often linearly distributed along coastlines or found in small pockets associated with river mouths, deltas, and the inland shores of barrier islands. This distribution results in a large edge effect that may reduce the isolation of tidal marsh and other habitats. Furthermore, as documented by Malamud-Roam et al. (*this volume*), tidal marshes have been highly unstable in their location and extension throughout recent geological history. Many of the largest areas of estuarine tidal marsh located at mid-latitudes are a consequence of flooding resulting from the sea-level rise associated with the melting of Pleistocene glaciers. The ice sheets covered arctic tidal marshes, among the most extensive in the world (Mitsch and Gosselink 2000). However, lower sea levels may have exposed more coastal plain and created a greater area of tidal marsh during the glacial maxima (G. Chmura, pers. comm.).

As we examine the species richness and endemism associated with tidal marshes in different regions, we will consider the following regional factors that might affect global patterns: the extent of tidal marsh habitat and its spatial distribution and the historical stability of tidal marsh and related habitats. Because information on these factors is either unavailable or difficult to synthesize for a number of important regions, the discussion will remain speculative and qualitative in nature. We begin with a brief discussion of marshes of different coastlines throughout the world based in large part on the classification system of Chapman (1977).

MAJOR AREAS OF TIDAL MARSHES

Global Overview

The lower marsh zone (between marsh edge and the mean high tide line) is dominated by one or two plant species whose physiognomy determines the overall structure of the simple habitat in terms of vegetation. Throughout the world, marshes differ in whether this lower zone is covered predominantly by cord grasses (*Spartina*) or, in areas with more arid climates or microclimates, by succulent halophytic plants, e.g., *Salicornia*, *Batis*, *and Suaeda*. Low marshes along the Pacific Rim, such as in Korea-Japan, California, Western Mexico, and those in southern Australia are generally covered by the succulent types of plants but eastern US and eastern South America are covered primarily with cord grasses. Lower marshes in Europe are often un-vegetated or have a sparse cover (Lefeuvre and Dame 1994).

Tidal marshes have patchy distributions (Fig. 1). Marshes form along low-energy shorelines that are associated with barrier islands along the outer coast or river mouths and estuaries. The extent and pattern of zonation in marshes is affected by the tidal patterns of their particular coastline. For most coastlines along open oceans, tidal ranges average between 1–2 m (NOAA 2004a, b, c, d). Marshes along the Atlantic and Pacific coasts of North America, southern coast of Australia, the North Sea, and the coast of Argentina generally experience these magnitudes of tidal flux. Along North American coastlines, tides increase as one moves northward. Certain isolated and shallow bodies of water—Baltic Sea of Europe, Laguna de Patos in Brazil, and Mediterranean and Caspian seas—experience very low tidal flux (NOAA 2004a, c). The shoreline of the Gulf of Mexico generally has small tidal amplitudes (0.5–1 m) compared to the Atlantic Coast (NOAA 2004a, b).

A few major estuaries are noteworthy because of the large areas of tidal salt and brackish marsh they support. San Francisco Bay in central California, which has three biologically relevant subdivisions (San Pablo, Suisun, and lower San Francisco bays), the Chesapeake and Delaware bays which flank the Delmarva Peninsula, and the estuary of the Río de la Plata along the eastern South American coast. These estuary systems represent the largest and most diverse tidal marshes in the world today. For example, approximately 90% of the original Pacific Coast wetlands from Cabo San Lucas to the Canadian border was found in the San Francisco Bay estuaries. By contrast, tectonically older coastlines with greater barrier island development usually have more continuous distribution of tidal marshes. The prime example of this can be found along the mid-Atlantic Coast of eastern North America. Along these coasts, marshes are concentrated in a few major estuaries. Delaware Bay, Chesapeake Bay, and Pamlico Sound estuaries contain 45% of the saltmarshes along the Atlantic Coast of North America, and the first two estuaries contain over three-quarters of the mid-Atlantic marshes (Field et al. 1991).

The major estuaries of temperate coasts are recent formations with similar histories. The history of the San Francisco Bay estuaries is explored fully in Malamud-Roam et al. (*this*

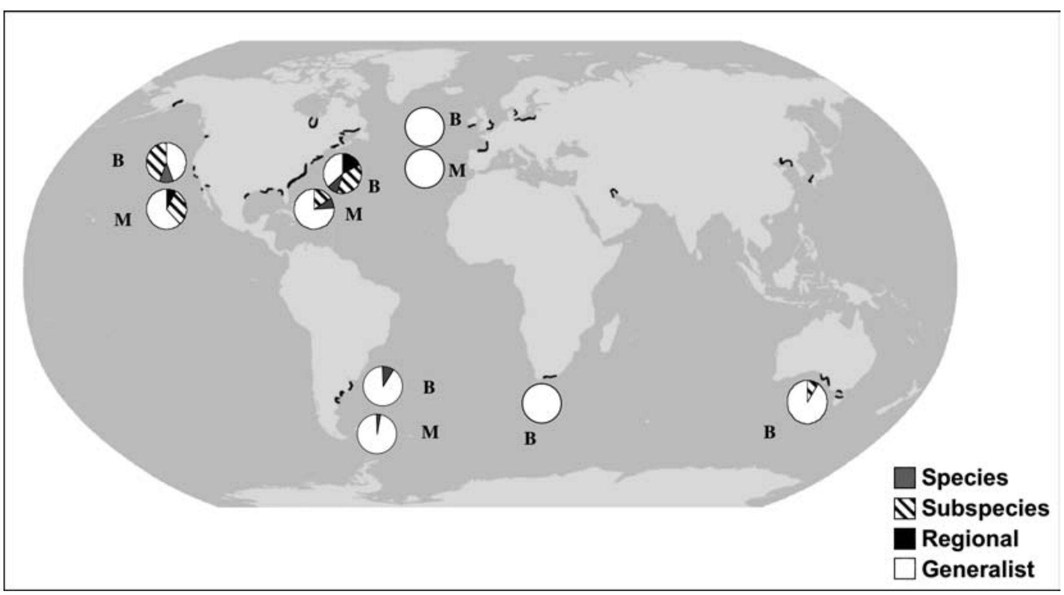

FIGURE 1. The world distribution of tidal marshes. The map is based on Chapman (1977), with revisions using more recent information on the distribution and quantity of tidal marsh along different coastlines. Circles indicate the proportion of native species of birds and mammals along different major coastlines with different levels of differentiation for tidal-marsh habitats. Tidal marsh includes brackish to salt and excludes tidal fresh water marsh.

volume). The Chesapeake Bay experienced a similar rapid development between 12,000 and 8,000 yr before present (BP), stabilizing into its present form at 3,000 yr BP (Colman and Mixon 1988, Bratton et al. 2003). Approximately 14,000 yr BP, river channels in the deltas of the Rio de la Plata and Rio Grande do Sul in South America drained to the edge of the continental shelf. At about 11,000–6,000 yr BP the sea shore moved westward across the coastal plain, shallow brackish bays developed in what would become the current estuarine valley. In the last 4,000 yr, as the sea levels became stable, coastlines became accretional, and areas of shallow coastal plain bordered the major portions of the estuary and adjacent Atlantic coastline accompanied the formation of protective sandbars (Urien et al.1980, Lopez-Laborde 1997).

These recently formed estuaries not only provide long protected shorelines adjacent to shallow coastal plains ideal for the formation of large areas of tidal marsh, but also tidal flux is generally greater in estuaries, and this, together with the mixing of salt and fresh waters over a large area, leads to the formation of more heterogeneous marsh communities and increased marsh zonation.

North American East and Gulf Coasts

Temperate-zone tidal marshes are by far the most extensive along the eastern and southern coasts of North America where they currently cover ca. 15,000 km^2, primarily along the southeast Atlantic and Gulf coasts (Field et al. 1991). The Gulf Coast supports ca. 9,880 km^2 of tidal marsh, with concentrations in the Mississippi delta. The remaining 5,000–6,000 km^2 are found along the Atlantic Coast, half along the south coast, 42% in the mid-Atlantic region, and the 8% in New England and the Canadian Maritimes (Field et al. 1991; Hanson and Shriver, *this volume*). Because of the lower tidal influx and the outflow from the Mississippi River, >40% of the Gulf Coast tidal marshes are brackish. The proportion of brackish marshes is well below 10% for other North American coastlines. Unlike most other regions, the lower tidal zones of eastern North America are naturally dominated by grasses of the genus *Spartina*, particularly smooth cordgrass (*Spartina alterniflora*), and not by members of the Chenopodiaceae, such as *Salicornia*. Upper zones of marshes are often a mix of several saltmeadow cordgrass (*Spartina patens*) with big cordgrass (*S. cynosuroides*) in the south and Townsend's cordgrass (*S. townsendii*) in the north, salt grass (*Distichlis spicata*) with marsh elder (*Iva frutescens*), and *Baccharis* shrubs. Brackish marshes along upper estuaries also support black needlerush (*Juncus roemerianus*), cattails (*Typha*), bulrushes (*Schoenoplectus*), and other rush species (*Juncus*). along with a number of forbs. East Coast marshes have been altered by changes in hydrology and nutrient influx and the overall result is the increased dominance of high marsh by the common reed (*Phragmites australis*) and, in low to mid-marsh, the spread of smooth cordgrass at the expense of a diversity of other high-marsh grasses and forbs (Bertness et al. 2002).

Along the southern Atlantic and Gulf coasts, the lower-marsh zone is dominated by smooth cordgrass which occurs patchily through the Caribbean and along the tropical South American coast to Argentina, where it, once again, dominates low, saline marshes. The upper, more brackish zones are dominated by black needlerush. Some of the largest concentrations of tidal marsh in the world are found along the mid- to south Atlantic and Gulf Coasts of North America.

North American West Coast

Tidal marshes of the West Coast of the US are limited in extent (ca. 440 km^2) of which ca. 70% are associated with the San Francisco Bay. Other small pockets are associated with a few other major estuaries such as Willapa Bay, Puget Sound, and river mouths (Field et al. 1991). The San Francisco Bay and delta estuary encompass <7% (4,140 km^2) of the land area in California but drain more than 40% (155,400 km^2) of its surface (Nichols et al. 1986). A band of *Salicornia* with a narrow outer zone of California cordgrass (*Spartina foliosa*) dominates the lower tidal zones, with a diversity of other plant species found in the upper zones (*Grindelia*, *Atriplex*, *and Baccharis*, among others). Brackish marshes, such as those of Suisun Bay and the lower Sacramento delta, are dominated by species of rush (*Schoenoplectus* and *Bolboschoenus* spp. and *Juncus* spp.). This represents one of the largest remaining areas of habitat for tidal-marsh vertebrates, yet the tidal marshes have been dramatically altered since the middle of the 19th century. Although efforts to restore ecological functions are underway, numerous threats to both endemic and widespread marsh organisms are still present, including habitat loss (Takekawa et al., chapter 11, *this volume*). Furthermore, invasive *Spartina* species (common cordgrass [*Spartina alterniflora*] and dense-flowered cordgrass [*Spartina densiflora*]) are encroaching on tidal flats and lower marsh edge (Gutensbergen and Nordby, *this volume*).

Tiny pockets of coastal marsh dominated by California cordgrass (with ample tidal flushing) and *Salicornia* spp. can be found along the southern and Baja California coasts (Field et al. 1991, Baja California Wetland Inventory 2004) and along the Mexican mainland from the mouth of the Colorado River south through Sinaloa. The isolated and localized marshes of southern California have suffered from urban development (Zedler et al. 2001; A. Powell, *this volume*), fragmentation, and changes in hydrology, thereby favoring monocultural patches of pickleweed.

Britain and Northern Europe

Tidal marshes in Europe are found around estuaries in the British Isles as well as along the coasts of the Waddell and Baltic Seas. The area of European coastal marshes is ca. 450 km^2 for the British Isles and 950 km^2 for the rest of western Europe (Dijkema 1990). These are high estimates as the areas of adjacent water bodies are included. Additional pockets of coastal marsh are found along the Mediterranean Sea and Persian Gulf (Chapman 1977). Large marshes (here defined as >5 km^2) are relatively uncommon, ca. 25 in Great Britain and 50 along the European mainland. Marshes in northern Europe respond to a sharp salinity gradient, from the coasts of the eastern Atlantic with salinity levels equivalent to full sea water to the barely brackish (0–5 ppt) marshes of the Baltic Sea.

European marshes have been diked, grazed, and harvested for hay since their most recent post-glacial development began (Hazelden and Boorman 2001). It has been estimated that 70% of the remaining European saltmarsh are thus exploited (Dijkema 1990). The original extent of tidal marsh may have been on the order of 1,000 km^2 for Great Britain and 3,000 km^2 along the northern European mainland.

European marshes show patterns of zonation that differ from other regions. Low areas of marsh are often devoid of vegetation, unlike North American marshes (Lefeuvre and Dame 1994). Mid-marsh zones are often now dominated by *Spartina* which has spread considerably, particularly along the British Isles, with the advent of Townsend's cordgrass and the hybrid common cordgrass or in more sandy areas by *Salicornia*, with upper zones covered with *Puccinellia*, *Juncus*, *Schoenoplectus*, *Carex*, and *Festuca* with patches of *Phragmites* reeds along the upper edges. Because of variation in soil type, tidal action, salinity, and long histories of human use, European marshes show considerable geographic variation in composition and zonation. For example, marshes in Scandinavia are dominated by grasses (*Puccinellia maritima*, *Festuca rubra*, and *Agrostris stolonifera*); they are referred to as salt meadows and have been heavily grazed. By contrast, Mediterranean marshes have a greater representation by *Salicornia, Salsola*, and *Suaeda* spp. (Chapman 1977) and are rarely grazed.

Eastern South America

Salt and brackish coastal marshes are largely restricted to the large shoreline of protected lagoons in Rio Grande do Sul, Brazil, and along estuaries in the Rio de la Plata of Argentina and Uruguay. Although we have an incomplete assessment of the quantity of such coastal marsh, recent estimates based on remote sensing and geographic information services suggest that Argentina alone has >2,000 km^2 (Isacch et al. 2006). The area of saltmarsh in Uruguay and Brazil is considerably smaller than this, perhaps on the order of 250 km^2 of which 150 km^2 is found at subtropical latitudes (C. S. B. Costa, unpubl. data). Floristically, these marshes resemble the marshes of southeastern US in their domination by smooth cordgrass in low marsh zones and a mixture of dense-flowered cordgrass, saltmeadow cordgrass, and *Distichlis* in higher zones. *Juncus* and *Bolboschoenus* dominate the interior zones with low salinity. The marshes along protected lagoons experience little tidal flux and their flooding is the result of less predictable wind (Costa et al. 2003). One of the largest South American tidal marshes is located in Bahía Samborombón Argentina. Extending from Punta Piedras to the northern point of Cabo San Antonio, Punta Rosa, it is included in the Depresión Del Salado region, which occupies practically the entire east-central portion of Buenos Aires Province. It encompasses about 150 km of coastline. Many channels and creeks as well as two main rivers—the Salado and the Samborombón—feed into this coastal area. The coastline of Bahía Samborombón has not yet felt the impact by human activity in the nearby pampas and grassland areas, because humans deem this area as suboptimal for cattle and other agricultural activities. Consequently, the tidal marsh areas have become refuges for many species that used to inhabit the large pampas grasslands and that are now not available for wildlife. In Bahía de Samborombón, salt grass, dense-flowered cordgrass, and *Sarcoconia ambigua* are the dominant plant species, with *Sporobolus indicus*, *Puccinellia glaucescens*, *Sida leprosa*, *Lepidium parodii*, *Spergularia villosa*, *Sisyrinchium platense* and *Paspalum vaginatum* as sub-dominant. This community also has large patches of pickelweed mixed with salt grass. At the mouths of rivers in flooded areas, smooth cordgrass is the dominant species and in partially flooded areas, smooth cordgrass is the common species.

Australia

Saltmarshes can be found locally along all Australian coastlines. The estimate for coastal saltmarsh area is 6,020 km^2 (N. Montgomery, pers. comm.), with the greatest extent of Australian saltmarshes found along the tropical coast in an adjacent zone to mangrove vegetation (Adam 1990). For example, only 660 km^2 (11%) of coastal marsh is found in New South Wales, Victoria, Tasmania, and South Australia combined (N. Montgomery, pers. comm.). Australia is unique among the continents in having the vast majority of its saltmarshes along tropical coastlines. Tropical saltmarshes are high level flats above mangroves—often hypersaline and with large salt flats and sparse vegetation (P. Adam, pers. comm.). In more favorable areas, flats are covered with grasses, such as *Sporobolus virginicus*. In general, tropical saltmarshes are restricted to sites that are too saline or are otherwise inhospitable for mangrove vegetation. Overall, Australia is sufficiently arid that streams are small and estuaries are few. In addition, much of the coastline of south Australia experiences small tidal ranges and much of the coastal marsh is found around coastal lagoons.

Mediterranean areas support sparse vegetation dominated by chenopod shrubs in the marshes along warm-temperate coastlines with more consistently moist conditions are limited in extent, but resemble marshes from other warm-temperate regions. Low marshes are characterized by *Sarcocornia quinquefolia* (Chenopodiacea) and the upper marshes by sedges and tall rushes. As in other regions, alien species are colonizing marshes with common cordgrass being the most invasive but thus far restricted primarily to Tasmania and Victoria (Adam 1990).

Asia

Tidal saltmarsh is found primarily in southwest Japan, along the Korean Peninsula and the shores of the Yellow Sea and shows a restricted distribution. We have not been able to obtain much quantitative information, but although Korea has extensive tidal flats, the total amount of saltmarsh may be <100 km^2, mostly dominated by flats of *Suaeda japonica* backed by *Phragmites* beds (N. Moore, pers. comm.). Despite a 50% decline in marsh area due to rice and salt production since 1950, the China coast still supports substantial areas of *Sueda*-dominated marsh, mostly along the yellow-sea. (Dachang 1996). Estimates for coverage are as high as 22,000 km^2. Native salt meadow is being invaded by *Spartina* from Europe and North America with there being now about 1,100 km^2 of this new habitat (Shuqing 2003). Lower marshes are locally dominated by *Suaeda*, *Zoysia*, and *Salicornia*, and upper marshes have a diversity of reeds (*Phragmites*, *Scirpus*) and shrubs (e.g., *Artemisia capillars*).

Africa

Most temperate saltmarsh in Africa is concentrated along the South African coast. This coast is generally exposed and only 18% of the 250 estuaries are permanently open to the sea (Colloty et al. 2000). The remaining estuaries are intermittently closed off as a result of reduced freshwater inflow and the development of a sandbar at the mouth. True inter-tidal saltmarshes, found in the permanently open estuaries comprise about 27 km^2 and tidal marsh in the closed (supra-tidal) systems account for 51 km^2. The total area in saltmarsh is, therefore, only 71 km^2. The inter-tidal marshes are dominated by small cordgrass *Spartina maritima, Sarcocornia perennis, Salicornia meyeriana, Triglochin bulbosa, Triglochin striata, Chenolea diffusa,* and *Limonium linifolium*. The dominant supratidal species are *Sporobolus virginicus, Sarcocornia pillansii,* and *Stenotaphrum secundatum* (Colloty et al. 2000).

METHODS FOR THE ANALYSIS OF DIVERSITY AND ENDEMISM

General Approach

The focus of the paper is terrestrial vertebrates. These include species that depend upon the marsh vegetation and the underlying substrate for a substantial part of their use of the tidal marsh habitats. Thus we exclude primarily aquatic species that may enter or feed in the channels and lagoons within tidal marshes, including fish, fish-eating and other birds feeding in aquatic habitats, mammals, and turtles. We also exclude strictly aerial-feeding taxa such as swallows, swifts, and bats. The line between aquatic and terrestrial species sometimes requires a subjective judgment. Among birds, for example, we have generally excluded herons, egrets, ibises, and other wading species, as well as waterfowl and most gulls and terns. We include songbirds, rails, and some species of shorebirds, such as Willets (*Catoptrophorus semipalmatus*), which have a substantial dependence upon the marsh vegetation itself for something more than roosting. The inclusion or exclusion of resident shorebirds from the list of tidal-marsh species is probably the most problematic of any group. When we turn to analysis we have restricted most to species that breed in tidal marshes. Among mammals, we exclude seals, sea otters, and cetaceans which feed in tidal channels and may rest upon tidal mud bars, but are primarily aquatic species.

Because this paper represents the first systematic compendium and classification of terrestrial vertebrates in tidal marshes, we used a diversity of sources as background information for our ecological classification. We relied primarily on the natural history literature for the major groups and supplemented this with information of knowledgeable informants and the gray literature as well. We were unable to obtain information from some areas, such as New Zealand, and the Black Sea, and therefore do not include faunas from such areas with small amounts of saltmarsh.

Species were classified into four groups, based on their demonstrable evolutionary specialization to tidal marsh habitats (Fig. 1): 1 = species that are largely or wholly restricted to tidal marshes; 2 = species that have recognized subspecies that are largely or wholly restricted to tidal marshes; 3 = species that have populations that are largely or wholly restricted to tidal marshes (these populations are not known to be differentiated); and 4 = species that occur in tidal marshes and other habitats as well. For species in the last two groups, we classified the dominant alternate habitats to tidal marsh: FM = fresh-water marsh and other fresh-water aquatic habitats, grass = grassland, agricultural fields and pastures and other open habitats, scrub = shrubby second-growth habitats, or varied = other non-tidal habitats. We designate which tidal-marsh species are known to regularly occur in salt as opposed to brackish marsh. This categorization is based largely upon the designation in the literature and not any controlled measurement or consistent criteria. However, we consider classifying species this way as providing a first approximation of which species occur in the most saline marshes. The following sections provide our major sources for the different higher taxa of vertebrates considered.

Amphibians and Reptiles

Nomenclature is based on (Uetz et al. 2005) and Frost (2004). We developed our habitat classification for amphibians and reptiles from several major natural history sources (Stebbins 1954, Conant 1969, Dunson and Mazzotti 1989, Ernst and Barbour 1989, Conant et al. 1998) as well as a lengthy review paper on the distribution of amphibians and reptiles in saline habitats throughout the world (Neill 1958). The review is the most comprehensive on this topic to date and is global in scope, but clearly focused more on North American and Europe than other saltmarsh regions although it has considerable information on mangrove swamp herpetofaunas. We therefore restrict our analysis for these classes to North America and the western Palearctic. In terms of a global assessment, the information on turtles is probably the most comprehensive.

Birds

Bird nomenclature is based on Sibley and Monroe (1990). Information on North American avifauna was obtained from the Birds of North America series (Poole 2006) and the field notes of the senior author, as well as more specialized accounts (Gill 1973, Benoit and Askins 1999). Habitat information on rails was based largely on Taylor (1998). Australian bird distributions were obtained from Higgins (1999), Higgins et al. (2001), and personal communications with several Australian ornithologists. Information on European and British birds was obtained from communications with John Marchant and Phil Atkinson, and found in Williamson (1967), Glue (1971) Greenhaugh (1971), Møller (1975), Larssen (1976), Spaans (1994), and more specialized references on particular taxa (Taillandier 1993, Allano et al. 1994). Information on Asian birds was based on Brazil (1991) as well as personal communications from Hisashi Nijati and Nick Moores. Information on the birds of South America was based on Wetmore (1926), Ridgely and Tudor (1989, 1994), Stotz et al. (1996), Martinez et al. (1997), Dias and Maurío (1998), Isacch et al. (2004) and communications from several South American ornithologists (Rafael Dias, Pablo Petracci, Santiago Claramunt, and Rosendo Fraga). Classification of birds of South Africa estuarine marshes was based on Hockey and Turpie (1999). Subspecific designations were based on Cramp (1988, 1992) and Cramp and Perrins (1993, 1994), American Ornithologists' Union (1957), Hellmayr (1932, 1938), Cory and Hellmayr (1927), and Hellmayr and Conover (1942), and Higgins (1999) and Higgins et al. (2001).

Mammals

Information on North American mammals was obtained by surveying reference materials containing range maps and varying details of habitat information, primarily Hall (1981), Wilson and Ruff (1999) and the mammalian species accounts of the American Society of

Mammalogy (<http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi/> [26 July 2006]). We also surveyed books dedicated to mammals of states where coastal tidal marshes were present: Álvarez-Castañeda and Patton (1999), Ingles (1967), Linzey (1998), Lowery (1974), Webster et al. (1985), and Williams (1979, 1986).

Published information for mammals that live in tidal-marsh ecosystems in South America is sparse. For this reason, we surveyed general field guides on Neotropical mammals (Emmons 1990) and books that had general distribution and habitat information for Neotropical mammals (Redford and Eisenberg 1992, Eisenberg and Redford 1999). Information was also obtained from field researchers with knowledge of the marsh ecosystems of the area (M. L. Merino and S. Gonzalez) and from reports and other unpublished literature (Milovich et al.1992, Merino et al. 1993, Yorio 1998, Bó et al. 2002). We also surveyed over 700 mammalian species accounts (<http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi/> [26 July 2006]) and searched for information regarding distribution and habitat use for mammals reported in or around the major marsh ecosystems of Argentina, Uruguay, and Brazil.

Information on European mammals was obtained from general reference materials such as Nowak (1999) as well as references that dealt exclusively with European and British mammals (Bjärvall and Ulström 1986, Mitchell-Jones et al. 1999). We also received anecdotal information from researchers that had experience surveying mammals in European marshes such as M. Delibes, J. Flowerdew, A. Grogan, R. Strachan, R. Trout, and D. W. Yalden.

Compared to North America and Europe, little is known about tidal-marsh mammals in Asia, Africa, and Australia. Therefore we do not include information in this review from these areas.

RESULTS

Tidal-Marsh Faunas

Amphibians and reptiles

We were able to locate references to 43 species of amphibians and reptiles regularly found in tidal marshes in North America (Table 1). However, the only saltmarsh taxa characteristic of saltmarshes outside of North America we were able to document were two species of saltmarsh inhabiting skinks (*Egernia*) in Australia (Chapple 2003). Within North America, 37 of the 41 North American species are restricted to the Atlantic or Gulf coasts. In his review, Neill (1958) emphasized that Florida was a particularly important area for finding salt-marsh populations of reptiles and amphibians. Despite the large number of species that have been found, at least locally, to inhabit tidal marshes, only colubrid snakes and emydid turtles have species or subspecies that were restricted to tidal marsh and adjacent estuarine habitats. Of the 13 species of snakes that have been reported from tidal marshes, three have subspecies restricted to tidal marshes or mangroves—northern water snake (*Nerodia sipedon*) and saltmarsh snake (*N. clarkia* [Myers 1988, Lawson et al. 1991, Gaul 1996]) and brown snake (*Storeria dekayi* [Anderson 1961]); the subspecies involved are found in the southeastern US. Similarly, one of the ten species of turtles that have been found in tidal marshes is restricted to estuarine habitats diamondback terrapin (*Malaclemys terrapin*). American crocodiles (*Crocodylus acutus*) are generally restricted to brackish or salt-water estuarine habitats, but predominantly occupy subtropical to tropical mangrove swamps.

Birds

The number of breeding tidal marsh birds varied between eight and 21 for the different continents with the highest number of species in the North and South American tidal marshes (Tables 2–6; Fig. 2a). However, the number of species found in saltmarsh was highest for North America (11), with other continents ranging between six–eight species. In the case of South Africa, the data were not available to categorize species as brackish or salt marsh and this region is not included in analyses for which this distinction is involved. The number of endemic species (two) and the number of species with at least one endemic subspecies (11) was highest for North America. In fact, we found only one endemic species or species with endemic subspecies outside of North America involving a single subspecies of the Slender-billed Thornbird (*Acanthiza iredalei rosinae*; Mathew 1994). Research is underway to determine if two species of South American saltmarshes (Bay-capped Wren-spinetail [*Spartonoica maluroides*] and the Dot-winged crake [*Porzana spiloptera*]) might have locally differentiated populations. The Zitting Cisticola (*Cisticola juncidis*) is found in, but not restricted to, tidal marshes in southern Europe, Africa, Asia, and Australia and should be examined, as well, for local differentiation. In North America, endemism is somewhat greater along the East Coast where two endemic species and six species with at least one endemic

TABLE 1. SPECIES OF TIDAL-MARSH AMPHIBIANS AND REPTILES OF NORTH AMERICA.

Species	Family	Class[a]	Coast[b]	Saltmarsh[c]	Alternate habitat[d]
Southern chorus frog (*Pseudacris nigrita*)	Hylidae	4	ENA	+	Varied
Spotted chorus frog (*Pseudacris clarkii*)	Hylidae	4	ENA	+	Grass
Little glass frog (*Pseudacris ocularis*)	Hylidae	4	ENA	+	FM
Green tree frog (*Hyla cinerea*)	Hylidae	4	ENA		FM
Gray tree frog (*Hyla versicolor*)	Hylidae	4	ENA		FM
Pine woods tree frog (*Hyla femoralis*)	Hylidae	4	ENA		Varied
Eastern narrow-mouthed toad (*Gastrophryne carolinensis*)	Microhylidae	4	ENA		Varied
Southern leopard frog (*Rana sphenocephala*)	Ranidae	4	ENA		FM
Pickerel frog (*Rana palustris*)	Ranidae	4	ENA		FM
Pig frog (*Rana grylio*)	Ranidae	4	ENA		FM
Common snapping turtle (*Chelydra serpentine*)	Chelydridae	4	ENA	+	FM
Spotted turtle (*Clemmys guttata*)	Emydidae	4	ENA		FM
Pacific pond turtle (*Emys marmorata*)	Emydidae	4	WNA		FM
Painted turtle (*Chrysemys picta*)	Emydidae	4	ENA		FM
Florida cooter (*Pseudemys concinna*)	Emydidae	4	ENA		FM
Florida redbelly turtle (*Pseudemys nelsoni*)	Emydidae	4	ENA		FM
Striped mud turtle (*Kinosternon baurii*)	Kinosternidae	4	ENA		FM
Eastern mud turtle (*Kinosternon subrubrum*)	Kinosternidae	4	ENA	+	FM
Green anole (*Anolis carolinensis*)	Iguanidae	4	ENA		Varied
Western mourning skink (*Egernia luctuosa*)	Scincidae	4	AUS	+	FM
Swamp skink (*Egernia coventryi*)	Scincidae	4	AUS	+	FM
Slender glass lizard (*Ophisaurus attenuatus*)	Anguidae	4	ENA	+	Grass
Saltmarsh snake (*Nerodia clarkia*)	Colubridae	1	ENA	+	
Northern water snake (*Nerodia sipedon*)	Colubridae	2	ENA	+	FM
West Mexican water snake (*Nerodia valida*)	Colubridae	4	WNA		FM
Mississippi green water snake (*Nerodia cyclopion*)	Colubridae		ENA		FM
Graham's crayfish snake (*Regina grahami*)	Colubridae	4	ENA		FM
Black swamp snake (*Seminatrix pygeae*)	Colubridae	4	ENA		FM
Common garter snake (*Thamnophis sirtalis*)	Colubridae	4	WNA		FM
Ring-necked snake (*Diadophis punctatus*)	Colubridae	4	WNA		Varied
Mud snake (*Farancia abacura*)	Colubridae	3	ENA	+	FM
Eastern indigo snake (*Drymarchon corais*)	Colubridae	4	ENA		Varied
Eastern racer (*Coluber constrictor*)	Colubridae	4	ENA		Varied
Rough green snake (*Opheodrys aestivus*)	Colubridae	4	ENA		FM
Eastern rat snake (*Elaphe obsoleta*)	Colubridae	4	ENA		Varied
Common king snake (*Lampropeltis getula*)	Colubridae	4	ENA		Varied
Eastern diamond-backed rattlesnake (*Crotalus adamanteus*)	Viperidae	4	ENA		Varied
Timber rattlesnake (*Crotalus horridus*)	Viperidae	4	ENA	+	FM
American crocodile (*Crocodylus acutus*)	Crocodylidae	3	ENA	+	FM
American alligator (*Alligator mississippiensis*)	Crocodylidae	4	ENA	+	FM

[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] Coast: W = west (Pacific) coast; E = east (Atlantic or Gulf) coast.
[c] + = regularly found in salt marsh (salinity ≈ sea water).
[d] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.

subspecies can be found, compared to the West Coast where no endemic species occur and five species have at least one endemic subspecies. Along the Gulf Coast, we found only one endemic species and four species with at least one endemic subspecies.

We focus our analysis on breeding birds, recognizing that a number of birds will appear in tidal marshes opportunistically during migration or winter periods. However, some species are relatively specialized on tidal marshes during the non-breeding season. For example, the endangered Orange-bellied Parrot (*Neophema chrysogaster*) over-winters largely in saltmarshes in southern Australia, where it feeds extensively on the seeds of *Halosarcia* and other chenopods (Loyn et al. 1986). In Britain and northern Europe, the

TABLE 2. SPECIES OF TIDAL-MARSH BIRDS OF NORTH AMERICA.

Species	Family	Class [a]	Coast [b]	Saltmarsh [c]	Alternate habitat [d]
Short-eared Owl (*Asio flammeus*)	Strigidae	4	W, E	+	FM, grass
Yellow Rail (*Coturnicops noveboracensis*)	Rallidae	4 NB [e]	E		FM, grass
Black Rail (*Laterallus jamaicensis*)	Rallidae	3 [f]	W, E	+	FM, grass
Clapper Rail (*Rallus longirostris*)	Rallidae	2	W, E	+	FM
King Rail (*Rallus elegans*)	Rallidae	4 NB [e]	E		FM
Virginia Rail (*Rallus limicola*)	Rallidae	4 NB [e]	W, E		FM
Willet (*Catoptrophorus semipalmatus*)	Scolopacidae	2	E	+	FM, grass
Northern Harrier (*Circus cyaneus*)	Accipitridae	4	W, E	+	FM, grass
Willow Flycatcher (*Empidonax traillii*)	Tyrannidae	4	E		FM, scrub
Song Sparrow (*Melospiza melodia*)	Fringillidae	2	W	+	FM, scrub
Swamp Sparrow (*Melospiza georgiana*)	Fringillidae	2	E		FM
Savannah Sparrow (*Passerculus sandwichensis*)	Fringillidae	2	W	+	Grass
Seaside Sparrow (*Ammodramus maritimus*)	Fringillidae	1	E	+	FM
Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*)	Fringillidae	1	E	+	
Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*)	Fringillidae	2	E	+	FM
Yellow Warbler (*Dendroica petechia*)	Fringillidae	4	E		FM, scrub
Common Yellowthroat (*Geothlypis trichas*)	Fringillidae	2	W, E	+ NB [e]	FM, scrub
Red-winged Blackbird (*Agelaius phoeniceus*)	Fringillidae	4	W, E	+	FM, varied
Boat-tailed Grackle (*Quiscalus major*)	Fringillidae	2	E	+	FM, varied

[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] Coast: W = west (Pacific) coast; E = east (Atlantic or Gulf) coast.
[c] + = regularly found in salt marsh (salinity ≈ sea water).
[d] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.
[e] NB = found primarily in non-breeding season.
[f] Black Rails might be considered tidal-marsh endemics, particularly the eastern subspecies, where inland breeding populations are very sporadic and small (Eddleman et al. 1994).

TABLE 3. SPECIES OF TIDAL-MARSH BIRDS OF EUROPE AND ASIA.

Species	Family	Class [a]	Saltmarsh [b]	Alternate habitat [c]
Short-eared Owl (*Asio flammeus*)			+	FM, grass
Water Rail (*Rallus aquaticus*)	Rallidae	4		FM
Redshank (*Tringa totanus*)	Scolopacidae	4	+	FM
Marsh Harrier (*Circus aeruginosus*)	Accipitridae	4		FM, grass
Bluethroat (*Luscinia svecica*)	Muscicapidae	4		Varied
Eurasian Penduline-Tit (*Remiz pendulinus*)	Paridae	4		FM
Zitting Cisticola (*Cisticola juncidis*)	Sylviidae	4		FM, grass
Middendorff's Grasshopper Warbler (*Locustella ochotensis*)	Sylviidae	4		FM
Japanese Marsh Warbler (*Locustella pryeri*)	Sylviidae	4		FM
Sedge Warbler (*Acrocephalus schoenobaenus*)	Sylviidae	4		FM
Eurasian Reed-Warbler (*Acrocephalus scirpaceus*)	Sylviidae	4		FM
Clamorous Reed-Warbler (*Acrocephalus stentoreus*)	Sylviidae	4		FM
Great Reed-Warbler (*Acrocephalus arundinaceus*)	Sylviidae	4		FM
Bearded Parrotbill (*Panurus biarmicus*)	Sylviidae	4		FM
Reed Parrotbill (*Panurus heuderi*)	Sylviidae	4		FM
Eurasian Skylark (*Alauda arvensis*)	Alaudidae	4	+	Grass
Horned Lark (*Eremophila alpestris*)	Alaudidae	4		Grass
Yellow Wagtail (*Motacilla flava*)	Motacillidae	4	+	Grass
Twite (*Carduelis flavirostris*)	Fringillidae	4 NB [d]		FM, grass
Pallas's Bunting (*Emberiza pallasi*)	Fringillidae	4		FM
Reed Bunting (*Emberiza schoeniclus*)	Fringillidae	4		FM
Lapland Longspur (*Calcarius lapponicus*)	Fringillidae	4 NB [d]	+	
Snow Bunting (*Plectrophenax nivalis*)	Fringillidae	4 NB [d]	+	

[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] + = regularly found in salt marsh (salinity ≈ sea water).
[c] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.
[d] NB = found primarily in non-breeding season.

TABLE 4. SPECIES OF BIRDS OF EASTERN SOUTH AMERICAN TIDAL MARSH.

Species	Family	Class [a]	Saltmarsh [b]	Alternate habitat [c]
Short-eared Owl (*Asio flammeus*)	Strigidae	4		Grass
Speckled Rail (*Coturnicops notatus*)	Rallidae	4		FM
Rufous-sided Crake (*Laterallus melanophaius*)	Rallidae	4		FM
Dot-winged Crake (*Porzana spiloptera*)	Rallidae	3	+	FM
Blackish Rail (*Pardirallus nigricans*)	Rallidae	4		FM
Plumbeous Rail (*Pardirallus sanguinolentus*)	Rallidae	4	+	FM
South American Painted-Snipe (*Nycticryphes semicollaris*)	Rostratulidae	4	+	FM
Long-winged Harrier (*Circus buffoni*)	Accipitridae	4		FM
Cinereous Harrier (*Circus cinereus*)	Accipitridae	4	+	FM
Spectacled Tyrant (*Hymenops perspicillatus*)	Tyrannidae	4		Grass
Sulphur-bearded Spinetail (*Cranioleuca sulphurifera*)	Furnariidae	4		FM
Yellow-chinned Spinetail (*Certhiaxis cinnamomea*)	Furnariidae	4		FM, mangroves
Hudson's Canastero (*Asthenes hudsoni*)	Furnariidae	4	+	FM, grass
Freckle-bearded Thornbird (*Phacellodomus striaticollis*)	Furnariidae	4		Scrub
Bay-capped Wren-Spintetail (*Spartonoica maluroides*)	Furnariidae	3	+	FM
Wren-like Rushbird (*Phleopryptes melanops*)	Furnariidae	4		FM
Sedge Wren (*Cistothorus platensis*)	Trogolodytidae	4	+	FM, grass
Correndera's Pipit (*Anthus correndera*)	Motacillidae	4		Grass
Grassland Yellow Finch (*Sicalis luteola*)	Fringillidae	4		Grass
Great Pampa-Finch (*Embernagra platensis*)	Fringillidae	4		Grass
Yellow-winged Blackbird (*Agelaius thilius*)	Fringillidae	4	+	FM

[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] + = regularly found in salt marsh (salinity ≈ sea water).
[c] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.

TABLE 5. BIRD SPECIES OF AUSTRALIAN TIDAL MARSHES.

Species	Family	Class [a]	Coast [b]	Saltmarsh [c]	Alternate habitat [d]
Grass Owl (*Tyto capensis*)	Tytonidae	4	N, E		Grass
Buff-banded Rail (*Gallirallus phillipensis*)	Rallidae	4	All		FM
Lewin's Rail (*Lewinia pectoralis*)	Rallidae	4	S, E		FM
Australian Crake (*Porzana fluminea*)	Rallidae	4	S, E	+	FM
Blue-winged Parrot (*Neophema chrysostoma*)	Psittacidae	4 NB			Scrub
Rock Parrot (*Neophema petrophila*)	Psittacidae	4 NB			Scrub
Orange-bellied Parrot (*Neophema chrysogaster*)	Psittacidae	4 NB			Scrub
Swamp Harrier (*Circus approximan*)	Accipitridae	4	All		FM, grass
White-winged Fairywren (*Melurus leucopterus*)	Maluridae		S, W	+	Scrub
Red-backed Fairywren (*Malurus melanocephalus*)	Maluridae		N, E		Scrub
Singing Honeycreeper (*Lichenostomus virescens*)	Meliphagidae	4	N, E, S		Scrub
Orange Chat (*Epithianura aurifrons*)	Meliphagidae		W	+	Scrub
White-fronted Chat (*Epthianura albifrons*)	Meliphagidae	4	S	+	Scrub
Slender-billed Thornbill (*Acanthiza iredalei*)	Pardalotidae	2	S	+	Scrub
Zitting Cisticola (*Cisticola juncidis*)	Sylviidae	4	N, W		Grass
Brown Songlark (*Cincloramphus cruralis*)	Alaudidae	4	E, W, S		Grass
Australasian Pipit (*Anthus novaseseelandiae*)	Passeridae	4	All		Grass

[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] Coast: N = north; S = south; W = west (Pacific) coast; E = east (Atlantic) coast.
[c] + = regularly found in salt marsh (salinity ≈ sea water).
[d] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.

Twite (*Acanthis flavirostris*), Snow Bunting (*Plectrophenax nivalis*), Lapland Longspur (*Calcarius lapponicus*), and Meadow Pipit (*Anthus pratensis*) are particularly noted for their dependence on saltmarshes in the winter; the Twite and other finches feed on the seeds of *Salicornia* (Brown and Atkinson 1996; J. Marchant, pers. comm.).

The endemic bird taxa include two species and the subspecies of four other species of sparrows and they all occur in North America. The endemic sparrow taxa are generally grayer with more

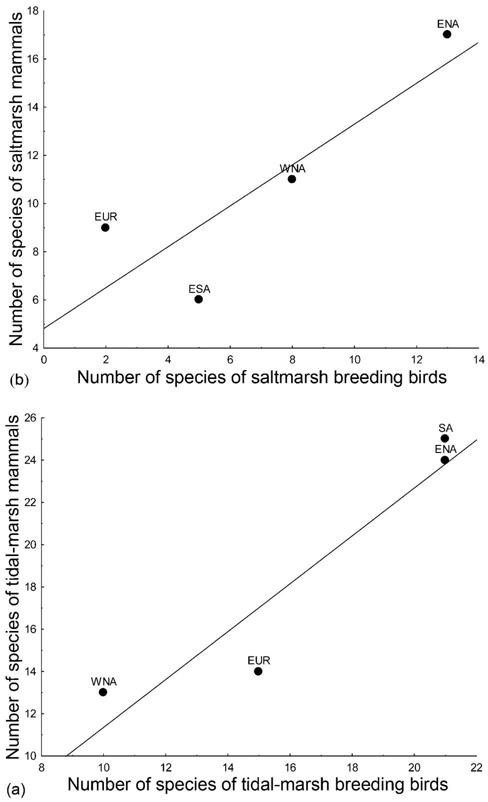

FIGURE 2. The number of species of native mammals plotted against the number of breeding birds for a single coastline associated with (a) tidal marshes and (b) salt marshes.

distinct black markings than the upland subspecies, and are also larger with relatively larger bills (Grenier and Greenberg 2005; Grenier and Greenberg, *this volume*). The bird species most restricted to saltmarshes is the Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*). A closely related species, the Nelson's Sharp-tailed Sparrow (*A. nelsoni*) occupies prairie wetlands, but has two isolated subspecies found in tidal marshes. Both occupy brackish and saltmarshes, as well as nearby freshwater meadows (Peters 1942, Greenlaw and Rising 1994) during the breeding season and saltmarshes in the winter. Seaside Sparrows (*Ammodramus maritima*) are also almost entirely restricted to saltmarsh, particularly low marsh dominated by smooth cordgrass. Two distinct Florida subspecies (*A. m. nigrescens* and *A. m. mirabilis*) are or were found in inland flooded prairie habitats in addition to *Spartina* marshes. Seaside Sparrows are characterized by their generally grayish coloration and a larger bill compared to related congeners.

Two species of *Melospiza* have distinct tidal-marsh subspecies. The Coastal Plain Swamp Sparrow (*M. georgiana nigrescens*) is found in brackish tidal marshes of the mid-Atlantic coast and is distinctly grayer, blacker, and has a larger bill than conspecific inland populations (Greenberg and Droege 1990). Three subspecies of Song Sparrows (*Melospiza melodia*) have been described for the San Francisco Bay estuaries (Marshall 1948b). These subspecies tend to be grayer, or in one case more yellow, than local upland Song Sparrows. The subspecies in the brackish Suisun Bay marshes (*M. m maxillaris*) has particularly black markings and a larger bill. Other endemic subspecies of birds have been described as darker than other populations, including the Salt-Marsh Yellowthroat (*Geothlypis trichas sinuosus*; Grinnell 1913) and the Slender-billed Thornbill (*Acanthiza iradelei rosinae*; Mathew 1994). Atlantic Coast subspecies of Marsh Wrens (*Cistothorus palustris*) have been reported to be grayer than inland subspecies (Kroodsma and Verner 1997). The saltmarsh subspecies of Savannah Sparrows (*Passerculus sandwichensis*) have been included with the Pacific coast *P. s. beldingi* group and the Large-billed Sparrow of the coast of the Gulf of California (*P. s. rostrata*; Rising 2001). The former is relatively grayish with heavy black markings; bill size varies clinally but is relatively slender compared to other Savannah Sparrows. Members of the *rostrata* group have large bills and are grayish with reduced streaking on the back.

Finally, the Clapper Rails (*Rallus longirostris*) tend to be small and gray compared to King Rails (*Rallus elegans*), with the West Coast Clapper Rails having a warmer rust coloration ventrally (more similar to King Rails) (Eddleman and Conway 1998). Clapper Rails are largely restricted to saltmarshes, except tropical populations along the west coast of Mexico, the Caribbean, and the Atlantic Coast of South America, which occupy mangrove swamps. The Black Rail (*Laterallus jamaicensis*) is often considered a salt-marsh-restricted species and occurs primarily in tidal areas, but small populations can be found in inland freshwater marshes (Eddleman et al. 1994). As a primarily saltmarsh bird, it shows the tendency towards melanism described for other taxa in this habitat.

Mammals

The number of native tidal marsh species ranges from 15 (Europe) to 25 (South America) to 35 (North America) for the different continents. When individual coastlines are considered, the east coast of South America has

TABLE 6. BIRD SPECIES OF SOUTH AFRICAN TIDAL MARSHES.

Species	Family	Class[a]	Alternate habitat[b]
Marsh Owl (*Asio capensis*)	Strigidae	4	Grass
Kaffir Rail (*Rallus caerulescens*)	Rallidae	4	FM
Red-chested Flufftail (*Sarothrura rufa*)	Rallidae	4	FM
Red-knobbed Coot (*Fulica cristata*)	Rallidae	4	FM
Black-winged Stilt (*Himantopus himantopus*)	Charadriidae	4	FM
Water Thick-knee (*Burhinus vermiculatus*)	Burhinidae	4	Grass
Yellow-billed Kite (*Milvus migrans*)	Accipitridae	4	Varied
African Bush-Warbler (*Bradypterus boboecala*)	Sylviidae	4	FM
Zitting Cisticola (*Cisticola juncidis*)	Sylviidae	4	Grass
Tinkling Cisticola (*Cisticola tinniens*)	Sylviidae	4	FM
Cape Wagtail (*Motacilla capensis*)	Motacillidae	4	Varied
Cape Longclaw (*Macronyx capensis*)	Motacillidae	4	FM

[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.

the highest species richness (25) followed by eastern North America (24) with lower values for Europe and western North America (15 and 14, respectively). In contrast, eastern North America has substantially more salt marsh species (excluding brackish marsh taxa) with 17; western North America has 10, Europe nine, and South America six. Endemic taxa are restricted to North America with the only entirely endemic species, the salt marsh harvest mouse (*Reithrodontomys raviventris*) occurring along the West Coast, and the West and East coasts each supporting four species that have at least one endemic subspecies.

North America has the most species of tidal-marsh mammals, yet these species comprise a small portion of the total fauna. Of the 90 species that have been reported in various habitats in coastal states from the eastern US and 167 from the Pacific coastal states, only 26% and 8%, respectively, are commonly present in brackish and/or saltwater tidal marshes (Table 7). These statistics apply to native species. In addition, exotic species such as the Virginia opossum (*Didelphis virginiana*; introduced to the West Coast), house mouse (*Mus musculus*), black rat (*Rattus rattus*), brown rat (*Rattus norvegicus*), house cat (*Felis catus*), and red fox (*Vulpes vulpes*; introduced in coastal southern California) are commonly found in tidal marshes. As far as we know, only in mammals do exotic species commonly inhabit tidal marshes and then only in North America. These species display a strong tendency to replace native species in tidal-marsh areas that have been altered and surrounded by human development (Takekawa et al. chapter 11, *this volume*). This case is most dramatic in disturbed tidal marshes in southern and central California where house mice and black rats have become the dominant small mammal species and harvest mice, meadow voles (*Microtus pennsylvanicus*) and shrews are either absent or occur in low densities (J. Maldonado, pers. obs.).

Endemism appears to be restricted to both coasts of North America. Despite the large number of tidal-marsh species in South American marshes, only one species, the pampas cat (*Felis colocolo*), is regionally restricted to tidal marshes (Table 8). In Europe we found a similar pattern, namely no endemic mammalian species or subspecies endemic to tidal marshes or species with regional populations restricted to tidal marshes. All species recorded as occurring in tidal marshes were species that inhabit both upland habitats and tidal marshes and their alternative habitat is freshwater marsh or grassland or else they are generalist species that used various habitats (Table 9).

On the Pacific Coast of California, the ornate shrew (*Sorex ornatus*) and vagrant shrew (*S. vagrans*) as well as western harvest mouse (*Reithrodontomys megalotis*) and California vole (*Microtus californicus*) have subspecies endemic to tidal marshes and most of these are restricted to tidal marshes in the San Francisco Bay, the Monterey Bay, and the southern California area (Rudd 1955, Thaeler 1961).

On the East Coast, the cinereus shrew (*Sorex cinereus*) has a subspecies (Tuckahoe masked shrew [*S. c. nigriculus*]) that is probably restricted to the salt-water littoral marshes of southern New Jersey (Green 1932). Two subspecies of the meadow vole, are associated with coastal saltmarshes. The Florida saltmarsh vole (*Microtus pennsylvanicus dukecampbelli*) is currently listed as endangered in the state of Florida (Florida Fish and Wildlife Conservation Commission 2004) and was originally reported

TABLE 7. SPECIES OF TIDAL-MARSH MAMMALS OF NORTH AMERICA.

Species	Family	Class [a]	Coast [b]	Saltmarsh [c]	Alternate habitat [d]
Virginia opossum (*Didelphis virginiana*) [e]	Didelphidae	4	E, W	+	Varied
Cinereus shrew (*Sorex cinereus*)	Soricidae	2	E	+	
Ornate shrew (*Sorex ornatus*) [f]	Soricidae	2	W	+	
Vagrant shrew (*Sorex vagrans*) [f]	Soricidae	2	W	+	
Southeastern shrew (*Sorex longirostris*)	Soricidae	4	E		FM
Marsh shrew (*Sorex bendirii*)	Soricidae	4	W	+	Varied
Northern short-tailed shrew (*Blarina brevicauda*)	Soricidae	4	E	+	FM
Least shrew (*Cryptotis parva*)	Soricidae	4	E	+	FM
Desert shrew (*Notiosorex crawfordi*)	Soricidae	4	W	+	Scrub
Eastern mole (*Scalopus aquaticus*)	Talpidae	4	E		Varied
Broad-footed mole (*Scapanus latimanus*)	Talpidae	4	W		Varied
Swamp rabbit (*Sylvilagus aquaticus*)	Leporidae	2	E	+	
Marsh rabbit (*Sylvilagus palustris*)	Leporidae	3	E	+	FM, grass
Brush rabbit (*Sylvilagus bachmani*)	Leporidae	4	W		Varied
Salt marsh harvest mouse (*Reithrodontomys raviventris*)	Muridae	1	W	+	
Western harvest mouse (*Reithrodontomys megalotis*)	Muridae	2	W	+	
Eastern harvest mouse (*Reithrodontomys humulis*)	Muridae	4	E	+	Varied
California vole (*Microtus californicus*)	Muridae	2	W	+	
Meadow vole (*Microtus pennsylvanicus*)	Muridae	2	E	+	
Long-tailed vole (*Microtus longicaudus*)	Muridae	4	E		FM
Townsend's vole (*Microtus townsendii*)	Muridae	4	E	+	FM, grass
Muskrat (*Ondatra zibethicus*)	Muridae	4	E	+	FM
Marsh rice rat (*Oryzomys palustris*)	Muridae	4	E	+	FM
Round-tailed muskrat (*Neofiber alleni*)	Muridae	4	E	+	Grass
Eastern woodrat (*Neotoma floridana*)	Muridae	4	E	+	Varied
White-footed mouse (*Peromyscus leucopus*)	Muridae	4	E		Varied
House mouse (*Mus musculus*) [e]	Muridae	4	E, W	+	Varied
Black rat (*Rattus rattus*) [e]	Muridae	4	E, W	+	Varied
Brown rat (*Rattus norvegicus*) [e]	Muridae		E, W	+	Varied
Nutria (*Myocastor coypus*) [e]	Muridae	4	E	+	FM, grass
Gray fox (*Urocyon cinereoargenteus*)	Canidae	4	E		Varied
Red fox (*Vulpes vulpes*) [e]	Canidae	4	E, W		Varied
Coyote (*Canis latrans*)	Canidae	4	E, W		Varied
Northern raccoon (*Procyon lotor*)	Procyonidae	4	E, W	+	FM
American mink (*Mustela vison*)	Mustelidae	3	E	+	Varied
Northern river otter (*Lontra canadensis*)	Mustelidae	4	E		Varied
Striped skunk (*Mephitis mephitis*)	Mustelidae	4	E, W	+	Varied
Domestic cat (*Felis catus*) [e]	Felidae	4	E, W	+	Varied
Horse (*Equus caballus*) [d]	Equidae	4	E	+	Varied
White-tailed deer (*Odocoileus virginianus*)	Cervidae	2	E	+	
Elk (*Cervus elaphus*)	Cervidae	4	W	+	Varied
Sika deer (*Cervus nippon*) [e]	Cervidae	4	E	+	Varied [c]

Note: Taxonomic arrangement of mammals in table as in Nowak (1999) and common and scientific names are based on Wilson and Reeder (1993).
[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] Coast: W = west (Pacific) coast; E = east (Atlantic or Gulf) coast.
[c] + = regularly found in salt marsh (salinity ≈ sea water).
[d] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.
[e] Non-native species: Virginia opossum and red fox native on the east coast.
[f] Taxonomy based on Hall (1981) but its designation is controversial (Chan et al., *this volume*).

to be restricted to a single population in a saltmarsh near Cedar Key, Florida (Wood et al. 1982). More recently, an additional population was discovered from a location 19 km north of the first population at the Lower Suwannee National Wildlife refuge in Levy County Florida (USDI Fish and Wildlife Service 2004). The other subspecies of meadow vole (*Microtus pennsylvanicus nigrans*) is common and has been reported from the uplands as well as tidal marshes in eastern Virginia and Maryland. Both subspecies have been described as being darker than conspecifics. A third isolated saltmarsh population of meadow vole occurs in the Santee delta of South Carolina, but its taxonomic status has not yet been studied (W. Post, pers. comm.).

TABLE 8. SPECIES OF TIDAL-MARSH MAMMALS OF EASTERN SOUTH AMERICA.

Species	Family	Class[a]	Saltmarsh[b]	Alternate habitat[c]
Lutrine opossum (*Lutreolina crassicaudata*)	Didelphidae	4		Varied
White-eared opossum (*Didelphis albiventris*)	Didelphidae	4		Varied
Southern long-nosed armadillo (*Dasypus hybridus*)	Dasypodidae	4		Varied
Screaming hairy armadillo (*Chaetophractus vellerosus*)	Dasypodidae	4		Varied
Large hairy armadillo (*Chaetophractus villosus*)	Dasypodidae	4		Varied
Torres's crimson-nosed mouse (*Bibimys torresi*)	Muridae	4		FM
Web-footed marsh rat (*Holochilus brasiliensis*)	Muridae	4		FM
House mouse (*Mus musculus*) [d]	Muridae	4	+	Varied
Black rat (*Rattus rattus*) [d]	Muridae	4	+	Varied
Brown rat (*Rattus norvegicus*) [d]	Muridae	4	+	Varied
Nutria (*Myocastor coypus*)	Muridae	4	+	FM
Swamp rat (*Scapteromys tumidus*)	Muridae	4	+	FM
Drylands vesper mouse (*Calomys musculinus*)	Muridae	4		FM, grass
Red hocicudo (*Oxymycterus rufus*)	Muridae	4		FM, grass
Azara's grass mouse (*Akodon azarae*)	Muridae	4	+	Grass
Bunny rat (*Reithrodon auritus*)	Muridae	4	?	Grass
Yellow pygmy rice rat (*Oligoryzomys flavescens*)	Muridae	4	+	Varied
Small vesper mouse (*Calomys laucha*)	Muridae	4		Varied
Brazilian guinea pig (*Cavia aperea*)	Caviidae	4		Varied
Capybara (*Hydrochaeris hydrochaeris*)	Hydrochaeridae	4	+	FM, grass
Plains viscacha (*Lagostomus maximus*)	Chinchillidae	4		Grass
Talas tuco tuco (*Ctenomys talarum*)	Ctenomyidae	4		FM
Common fox (*Dusicyon gymnocercus*)	Canidae	4		Varied
Molina's hog-nosed skunk (*Conepatus chinga*)	Mustelidae	4		Varied
Lesser grison (*Galictis cuja*)	Mustelidae	4		Varied
Pampas cat (*Felis colocolo*)	Felidae	3	+	Varied
Geoffroy's cat (*Felis geoffroyi*)	Felidae	4	?	Varied
Marsh deer (*Blastocerus dichotomus*)	Cervidae	4		FM, grass
Pampas deer (*Ozotoceros bezoarticus*)	Cervidae	4		Grass

Note: Taxonomic arrangement of mammals in table as in Nowak (1999) and common and scientific names are based on Wilson and Reeder (1993).
[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] + = regularly found in salt marsh (salinity ≈ sea water).
[c] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.
[d] Non-native species.

TABLE 9. SPECIES OF TIDAL-MARSH MAMMALS OF EUROPE.

Species	Family	Class[a]	Saltmarsh[b]	Alternate habitat[c]
Eurasian shrew (*Sorex araneus*)	Soricidae	4	+	FM, grass
Eurasian water shrew (*Neomys fodiens*)	Soricidae	4	+	FM, grass
Lesser shrew (*Crocidura sauveolens*)	Soricidae	4	+	Varied
European water vole (*Arvicola terrestris*)	Muridae	4		Varied
Field vole (*Microtus agrestis*)	Muridae	4	+	Varied
Eurasian harvest mouse (*Micromys minutus*)	Muridae	4		FM, grass
Long-tailed field mouse (*Apodemus sylvaticus*)	Muridae	4		Varied
House mouse (*Mus musculus*)	Muridae	4		Varied
Black rat (*Rattus rattus*)	Muridae	4	+	Varied
Brown rat (*Rattus norvegicus*)	Muridae	4	+	Varied
Least weasel (*Mustela nivalis*)	Mustelidae	4	+	Varied
European rabbit (*Oryctolagus cuniculus*)	Leporidae	4	+	Varied
European hare (*Lepus europeus*)	Leporidae	4	+	Varied
Sika deer (*Cervus Nippon*)	Cervidae	4	+	Varied

Note: Taxonomic arrangement of mammals in table as in Nowak (1999) and common and scientific names are based on Wilson and Reeder (1993).
[a] Class: 1 = endemic species; 2 = species with endemic subspecies; 3 = species with population locally restricted to tidal marsh; 4 = generalist.
[b] + = regularly found in salt marsh (salinity ≈ sea water).
[c] Alternate habitat (for generalists) FM = freshwater marsh or other aquatic habitat; grass = grasslands or fields; scrub = scrub habitats; varied = different habitats.

Two subspecies of mink (*Mustela vison lutensis* and *M. v. halilemnetes*), were originally described as being restricted exclusively to the saltmarshes of the Atlantic and Gulf Coasts, respectively (Bangs 1898). *M. v. halilemnetes* was described as being slightly paler than *M. v. lutensis* and somewhat paler than *M. v. vulgivaga* from Louisiana coastal marshes. However, these differences did not seem valid and *M. v. halilemnetes* has been lumped into the more widely distributed *M. v. lutensis* and *M. v. vulgivaga* is now recognized to be more widely distributed throughout Louisiana.

Northern raccoons (*Procyon lotor megalodus*) inhabiting the marshes of southern Louisiana have been described as being more yellowish with a more pronounced mid-dorsal line than adjacent subspecies. Specimens of the swamp rabbit (*Sylvilagus aquaticus littoralis*), from the gulf coasts of Texas, Louisiana, Mississippi, and Alabama, were described as being darker and more reddish brown than the nominate subspecies. The validity of this subspecies has been questioned, however. Specimens of the muskrat (*Ondatra zibethicus*), from the central Gulf Coast, assigned to the subspecies *O. z. rivalicus,* have been described as being darker than specimens from the northcentral and northeastern US (Willner et al.1980).

At least one subspecies of white-tailed deer (*Odocoileus virginianus mcilhennyi*), from the coastal marshes of Louisiana, has been described as being smaller, darker, and larger footed than upland populations (Miller 1928). Because of numerous introductions and relocations since the mid-1950s, current populations of deer in Louisiana do not reflect these patterns of geographic variation.

DISCUSSION

Endemism

Whereas most of the dominant plants of tidal marshes are restricted to tidal marshes or may occur locally in inland saline habitats (Chapman 1977), the terrestrial vertebrate fauna shows relatively little specialization. In fact, given the ecological distinctiveness of both tidal-marsh environment and its flora, the number of described endemic taxa of terrestrial vertebrates is surprisingly small. We know of five species restricted or largely restricted to coastal marshes and only 18 additional species with at least one subspecies so restricted. The 23 species were predominantly birds (11), followed by mammals (nine) and reptiles (three). No endemic taxa of amphibians are known from tidal marshes.

Why North America?

The most striking, and ultimately puzzling, pattern in the occurrence of endemism was its almost complete restriction to North American coastlines (Fig. 1). All but one of the 25 species showing complete or partial endemism were found in North America. The single exception is a subspecies of Australian songbird. Of these, 14 are species (or have subspecies) restricted to the Atlantic or Gulf Coasts and eight are found only along the Pacific Coast.

To be sure, these data are probably biased by the lack of geographic coverage for some areas. More fundamentally because the vast majority of endemic taxa are subspecies, the detection of such forms will vary with the thoroughness with which geographic variation has been assessed in different regions. Certainly, the uncovering of ecological races associated with tidal marshes in South America is still a possibility. However, we believe that differences in the thoroughness of taxonomists to describe subspecies does not account for differences among the faunas of Europe, Australia, and North America. It is likely that the level of descriptive taxonomy for birds and mammals even in South America is sufficiently high that tidal-marsh subspecies would have been described. The significance of saltmarsh subspecies was initially discussed by Grinnell (1913) and Wetmore (1926) was probably aware of these associations because he collected in the South American saltmarshes in 1920–1921.

The concentrations of endemic forms in North America is likely to be real, at least partially, and not just artifacts of collecting or taxonomy. Any explanation needs to account for characteristics of the Atlantic, Gulf Coast, and Pacific Coast tidal marshes, because endemics are associated with all. We have identified four hypotheses that might explain the high levels of endemism in North American tidal marshes:

1. Any post-glacial expansion of tidal marsh habitats in North American coastlines resulted in either higher quality or quantity of tidal-marsh habitat that would in turn be able to support large enough populations of colonizing species to allow rapid diversification to proceed.
2. Tidal-marsh habitats were more stable throughout the Pleistocene resulting in the minimization of the extinction of differentiated forms.
3. Tidal-marsh habitats have shown both greater expansion and stability through time (a combination of the first two hypotheses).

4. The North American fauna contained particular taxa that had characteristics that favored the successful colonization of and diversification in tidal marshes.

The first three hypotheses would result in different temporal patterns of divergence of tidal marsh forms. The first hypothesis would result in most tidal-marsh endemics having diverged over the past 5–10,000 yr as coastal estuarine marshes developed. The greater stability hypothesis 2 should result in a preponderance of taxa that diverged earlier in the Pleistocene. Hypothesis 3, the combined hypothesis, would be supported by a complex pattern of both older and more recently derived taxa.

The results of studies looking at genetic divergences between coastal-marsh vertebrates and upland conspecifics (Chan et al., *this volume*), suggest that the endemic taxa in North American tidal marshes have both ancient and very recent association with tidal marshes, supporting hypothesis 3. Of the 14 species or subspecies for which genetic divergence data are available, eight are Holocene (<8,000 yr BP, i.e., since the last glaciation), four date to the mid-Pleistocene (500,000–1,000,000 yr BP) and three apparently diverged during the Pliocene (1.8–8 million yr BP). This suggests that tidal marshes in North America have both provided stable refugia for few endemics throughout the Pleistocene, but have expanded rapidly enough after the last glacial maximum (LGM) to allow rapid evolution of morphological traits. The tendency, although the sample size is too small for formal analysis, is for the older taxa to have southern distributions (Seaside Sparrow, Savanna Sparrow, diamondback terrapin, and saltmarsh snake), which suggests that southern refugia along the Gulf of Mexico and Mexican coastlines may have played a role in reducing the probability of extinction.

What makes the higher degree of endemism in North America all the more puzzling is that the processes that lead to endemic forms in North America have operated along coastlines that are very different geologically (Malamud-Roam et al., *this volume*). Presently, the Atlantic and Gulf coasts of North America have the greatest aerial extension of coastal tidal marsh. The Pacific Coast is a tectonically younger and more active coastline than the East Coast and supports an overall limited amount of tidal marsh, making opportunities for adaptation and divergence less likely.

The pattern of divergence in North America suggests that in more northern areas, tidal-marsh refugia were not available for most vertebrate taxa and that the Pleistocene was an epoch that saw repeated extinction and recolonization along these coastlines. In contrast, the number of taxa with more southerly distributions suggests that these populations could retreat to tidal marshes through many or all of the Pleistocene glaciations. The discussion in Malamud-Roam et al. (*this volume*) makes it clear that lower sea levels, colder water temperatures, reduced sedimentation from river flow, and ice cover all combine to reduce the extent of tidal marshes during the glacial maxima. Therefore, for potential Pleistocene refugia we should look to areas with shallow protected coastlines, fresh water, sediment input, and moderate ocean temperatures (Chapman 1977). The Mississippi delta-gulf coast, certain areas in the South Atlantic, and the Gulf of California are all likely areas for such refugia (Malamud-Roam, pers. comm.). Conditions in the East were drier and the marsh systems would have received less sediment influx. However, it seems likely that delta and barrier island formations would have persisted. In contrast, southwestern North America saw wetter conditions with greater precipitation during the glacial periods (Thompson et al. 1993) and the Colorado River delta system would have drained the great inland alkali lakes and probably transported more sediment (Sykes 1937); cooler temperatures would have favored more diverse saltmarsh vegetation and shifted the marsh-mangrove transition southward (Chapman 1977). An analysis of these factors may explain the global patterns as well. For example, the major extensions of shallow, protected shorelines in Europe are along the glaciated northern edge of the continent, and most of the major river systems drain northward into these areas. At least from a superficial analysis, conditions appear much more favorable for Pleistocene coastal marsh formation in North America than at least the western Palearctic.

The appropriate taxa hypothesis (hypothesis 4) would predict that endemics would be from a few vertebrate families that possess some identifiable adaptation to tidal-marsh life. For example, the surprising lack of endemic avian taxa in tidal marshes of eastern South America, may in part reflect the paucity of emberizid finches (the main group displaying such endemism) in the Pampean faunal region (J. P. Isacch, pers. comm.). However, in general we believe that the lack of appropriate source taxa is not a convincing argument for why endemic forms are close to absent outside of North America. Although a few vertebrate genera are repeatedly involved in the development of endemic forms, this is to be expected because the occupancy of tidal marshes probably provides a number of ecological filters to possible colonizing species. The important point is that the different genera involved are themselves diverse and unremarkable as far as we know.

Specialization in Different Classes of Vertebrates

Brackish marshes, located at the higher tidal zones and the upper ends of estuaries, support the largest number of species and presumably require the least specialization to the tidal-marsh environment. We, therefore, consider the proportion of species found in true saltmarshes to be an indication of the degree of specialization on tidal marshes within a higher order taxonomic grouping. We have focused our attention on reptiles, birds and mammals. Comparing these classes of vertebrates, we find mammals comprised the greatest proportion of saltmarsh inhabiting taxa (44%), followed by reptiles (39%), birds (33%), and amphibians (16%).

Specialization and Differentiation

We found a clear relationship between the probability that a taxon will show some degree of differentiation and whether it occupies saltmarsh or is found only in brackish marsh. Considering reptiles, birds, and mammals, we find that 97% of the endemic species or endemic subspecies are found in saltmarsh. On the other hand, only 30% of the non-differentiated species occur in saltmarsh. Mammals stand out as having a large number of non-differentiated species that occupy saltmarshes. Removing mammals, only 16% of the non-differentiated vertebrates occur in saltmarshes. These results are non-circular, because it is entirely possible to have coastal marsh taxa that avoid saltmarshes and yet are morphological distinct from non-coastal marsh populations. The Coastal Plain Swamp Sparrow is an example of this. The results do suggest that species that occupy the extreme of the environmental gradient in saltmarshes are the ones most likely to have differentiated.

Patterns of Species Richness

We evaluate regional differences in species richness by comparing the faunas of a single continental coastline. We have data to compare mammals and birds and total tidal-marsh area of both coasts of North America, the coastline of Europe, and that of eastern South America. For the bird analysis, we included only the south coast of Australia, using an approximation of 600 km^2 for total marsh areas. The total number of native tidal-marsh species of birds and mammals was highly correlated across these different coastal areas (Fig. 2a; $r^2 = 0.93$, N = 4) with the highest species richness in eastern South America and North America and lowest in western North America. Furthermore, the total number of mammal and bird species occupying saltmarsh was also correlated (Fig. 2b; $r^2 = 0.73$, N = 4). However the number of saltmarsh birds and mammals was poorly correlated with the total number of tidal-marsh species.

The diversity of tidal-marsh mammals and birds appeared to be related to the overall area of tidal marshes along a particular coastline ($r^2 = 0.50$ for birds; $r^2 = 0.40$ for mammals). The number of saltmarsh species of mammals (Fig. 3; $r^2 = 0.71$) and birds ($r^2 = 0.55$) were more strongly correlated with total tidal marsh area. We have already seen that the tendency for differentiation of taxa was somehow related to the occupancy of true saltmarsh. The total number of endemic species and species with endemic subspecies was related to the number of saltmarsh species (Fig. 4; $r^2 = 0.72$) and unrelated to the number of tidal marsh species as whole ($r^2 = 0.02$).

Although general species-area relationships exist that emphasize the overall importance of current marsh area, some caution is necessary. First, these relationships are based on few data points (coastlines) and only birds and mammals. Second, and perhaps more importantly, the

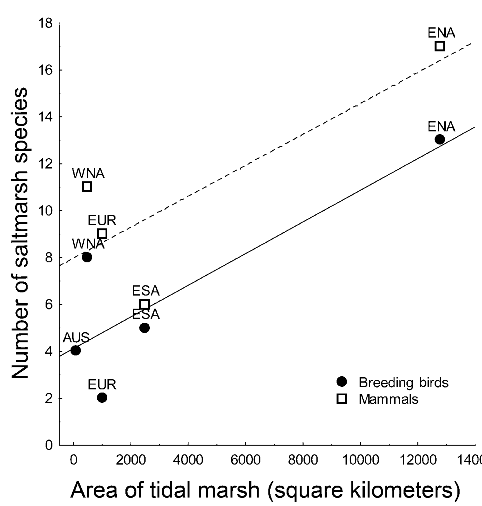

FIGURE 3. The number of species of native mammals and breeding birds plotted against tidal-marsh area for different coastline for saltmarsh species.

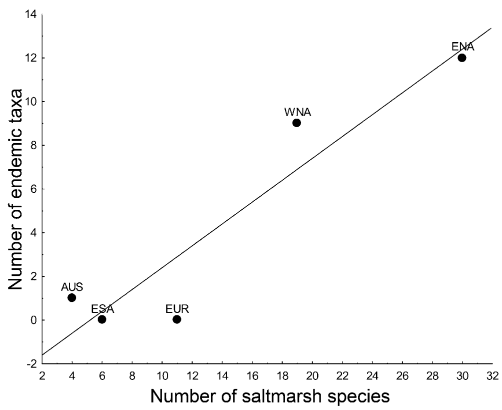

FIGURE 4. For native mammals and breeding birds, the number of endemic species (category 1) or species with at least one endemic subspecies (category 2) plotted against number of total saltmarsh mammal and breeding bird species (only bird species for Australia).

outliers may provide greater insight for future research than the general trends. For overall tidal marsh species, South America appears to have higher species richness than expected just based on marsh area alone. More interesting though is the much-higher-than expected species richness of both saltmarsh species and endemic taxa found in western North America when plotted against marsh area. As we stated in the section on endemic taxa, this cannot be explained by the size and diversity of habitats associated with an undisturbed San Francisco Bay system. A number of the taxa are associated with small marshes in the relatively marsh-free coastline of southern California.

Alternative Habitats

For non-specialist tidal-marsh vertebrates, the dominant alternative habitat is freshwater marsh and related aquatic habitats (49%) with grasslands and agricultural fields contributing another 29%. These figures vary considerably among major classes of vertebrates; for birds, amphibians, and reptiles, freshwater marsh comprises the major alternative habitat for 59–73% of the species. However, in mammals only 30% of the species are found commonly in freshwater marshes and a majority is found in grassland or a variety of other upland habitats. The lack of freshwater marsh species of mammals to colonize tidal marshes perhaps underscores the role of substrate flooding in the presence of small mammals in the most tidal of marshes.

Key Areas of Freshmarsh-Saltmarsh Interchange

We have discussed possible refugia for saltmarsh taxa that have persisted through the glaciations. The diversity of organisms that have colonized saltmarshes with or without diversification can be additionally explained by the potential of interaction of coastal marsh and interior marsh faunas. It is unclear whether any of the tidal-marsh regions outside of North America have such areas of extensive potential interchange, but one area to look in South America would be the wetlands associated with the Rio de la Plata connecting to interior wetlands in the La Plata Basin and the flooded pampas. La Plata basin is located in an area where significant freshwater and brackish water interactions may take place; it holds the largest wetlands in the world and has a wide variety flora and fauna associated with grasslands and wetlands. In North America, three areas stand out as having a long history of close contact or interdigitation of major fresh, brackish and saltwater wetlands. First, Odum (1953) and Neill (1958) focused on the Florida peninsula as an area of important interchange between freshwater and marine organisms. The low relief, large amount of freshwater flow, and changing sea levels have contributed to a continuous faunal interchange along the salinity gradient. Present day Florida has a very extensive brackish wetland system and many of the freshwater systems have a high concentration of dissolved chloride, which allows for the inland invasion of typically marine invertebrates. Neill (1958) noted that Florida supported an extraordinarily high number of salt and brackish marsh populations of reptiles and amphibians. Certain birds show freshwater-saltwater distributions where in other places in their range they are restricted to saltmarsh habitats (Seaside Sparrows and Boat-tailed Grackles [*Quizcalus major*]). A second region is the San Francisco Bay-delta-Central Valley wetland systems discussed by Malamud-Roam et al. (*this volume*). Prior to human manipulation of the hydrology of the region and also through the pluvial periods in western US, this region must have formed a large area of interchange between freshwater and brackish water wetlands. Western North America had extensive alkali and saline wetlands which may have provided source taxa for tidal marsh invasions. Finally, the coast of the Gulf of Mexico supports a large portion of the North American oligohaline marshes, particularly in the region of the Mississippi Delta.

Ecological Divergence in Tidal-Marsh Populations and Species

Saltmarsh forms often show high degrees of morphological, ecological and physiological differentiation, even though estuarine habitats are localized and not isolated from upland or freshwater habitats. Certain features of tidal-marsh life may provide exceptionally sharp selective gradients which ultimately favor assortative mating with individuals that can survive in saltmarsh habitats. Dunson and Travis (1994) made a convincing argument for the role of physiological adaptation to salinity as a driving force for divergence of saltmarsh animals.

As in the specialized saltmarsh flora, a major set of adaptations that distinguish tidal-marsh specialists is related to living in a highly saline environment. In general, estuarine species do not show as extreme a level of adaptation to saline environments as do more truly marine forms. For example, while sea-going reptiles and pelagic birds have salt glands which concentrate and excrete hypersaline solutions (Heatwole and Taylor 1987), only a few estuarine vertebrate taxa possess specialized salt glands. Clapper Rails have large nasal salt glands (Olson 1997) and the largely freshwater King Rail possesses smaller ones, even when both are raised in similar captive environments (Schmidt-Nielsen and Kim 1964). The fact that even the largely freshwater species possesses a salt gland suggests that the original evolution of salt glands in this rail complex occurred during an ancestral occupation of estuarine habitats prior to the recent colonization by Clapper Rails (Olson 1997). Passerine birds do not possess specialized salt glands, but show adaptation of kidney morphology and renal function, which include enlarged size including an increase in the number of medullary cones and an increase in the proportion of nephrons with loops of Henle. This results in an increased ability to concentrate salt (Goldstein, *this volume*)

By and large, tidal-marsh vertebrates are not as specialized for saline environments as are marine vertebrates. Estuarine snakes (e.g., *Nerodia clarkia*) are not known to have specialized glands, but have a relatively impermeable skin and are behaviorally adapted to obtain all of their moisture from their diet (Pettus 1958, 1963; Conant and Lazell 1973, Dunson and Mazzotti 1989). The behavioral difference is simple—tidal-marsh snakes do not drink salt water, whereas their freshwater relatives have no such inhibition. Nonetheless, the difference is sufficient to cause freshwater water snakes to die in salt water, where the tidal-marsh snakes survive. The same is true for turtles that inhabit tidal marshes—either as a specialist (diamondback terrapin Robinson and Dunson 1975) or generalist (common snapping turtle [*Chelydra serpentine*]; Dunson 1981, 1986)

Research on adaptation to salinity in tidal marsh mammals is more limited. Meadow voles from saltmarshes are apparently physiologically limited to ingesting water with <50% of the salinity of sea water (Getz 1966). They cannot consume large quantities of smooth cordgrass, which has tissue moisture with high salt concentrations. Saltmarsh inhabiting voles may obtain moisture from precipitation, dew, and from the tissue of less salty plants, such as saltmeadow cordgrass. Furthermore, Coulombe (1970) showed that the California vole was better able to consume halophytic plants than its performance on tests with saline drinking water would suggest. Although the physiological mechanism has not been studied, it appears that the salt marsh harvest mouse can survive longer ingesting more saline solutions than does the non-tidal marsh western harvest mouse (Fisler 1963, 1965). In several of the above studies, it was demonstrated that mice from freshwater marshes either showed evidence of weight loss or mortality when presented higher salinity water but see MacMillen (1964). Other adaptations to salinity are behavioral, including the possible use of torpor under conditions of osmotic stress (Coulombe 1970). The presence of physiological and behavioral adaptations in saltmarsh forms suggests that selection against hybrids between inland and salt populations may be intense and forms the basis for ecological separation and perhaps to speciation. This may go a long way towards explaining why differentiated forms tend to be specifically associated with salt rather than brackish tidal marsh.

A sharp discontinuity in predominant substrate color (often related to the concentration of sulphates in sea water) may also provide a strong selective force against hybrids and thus shape morphological divergence, even in the face of ongoing gene flow. As discussed by Grenier and Greenberg (*this volume*), many saltmarsh forms tend to be melanistic, displaying both grayer and blacker coloration. Presumably this is related to local cryptic adaptation to saltmarsh substrates and hence may contribute to enforcing diversification in tidal marsh forms. Since Grinnell's (1913) classic paper on estuarine vertebrates, saltmarsh melanism has been documented in a number of avian and mammalian taxa. We have documented melanistic populations of shrews, voles, and harvest mice in our discussion of endemic mammals. For example, several endemic subspecies of small mammals were originally described as new in southern California partially because of their darker pelage coloration (Von Bloeker 1932). Neill (1958) noted a number of examples of local melanism associated with tidal marsh reptiles and amphibians. More recently, melanistic subspecies of water snakes have been described for the *Spartina* and *Juncus* marshes of coastal North Carolina (Conant and Lazell 1973). Later Gaul (1996), for example, found a strong correlation between degree of melanism and the salinity of the water in a tidal marsh in the common water snakes of coastal North Carolina. The gulf salt marsh snake (*Nerodia clarkia clarkia*) is reported to have more evenly dark dorsal lines with less patterning (Pettus 1963; Myers 1988), which may be an adaptation to the lack of blotchy patterning in tidal muds. It may also, as the author suggested, blend in with the striped patterning of grassy marsh vegetation.

CONCLUSIONS

Although many vertebrates use brackish or saline tidal marshes from time to time, the number of species that are commonly resident in the marshes is generally small and the number that occurs regularly in saltmarshes is even smaller. In mammals and birds the number of species that use tidal marshes along a particular coastline is related to the current amount of tidal marsh. Despite a fairly strong suite of environmental differences, tidal marshes support relatively few endemic species, i.e., species that are wholly or largely restricted to these marshes.

Overall the greatest number of species and the most endemic taxa of tidal marshes are found in eastern North America. Fewer endemic taxa are found along the West Coast of North America, primarily in the San Francisco Bay, but also in the smaller marshes of the southern California and Mexican coastlines. Surprisingly, the only endemic taxon we have been able to locate outside of North America is a subspecies of Australian thornbird. Oscine passerines, and in particular the emberizine sparrows, have the largest number of endemic taxa. Other groups with multiple endemics are the shrews, murid rodents, and colubrid snakes.

The probability that a taxon is endemic or has endemic subspecies in tidal marshes is related to its occupancy of salt as opposed to brackish marshes. This is not surprising considering that the characters that show divergence are behavioral and physiological adaptations to cope with salinity and shifts in coloration to blend in with the dark acid-sulfate soils. These ecosystem characteristics, along with major changes in invertebrate communities and patterns of plant production and seed set co-vary and reinforce differentiation along the fresh to saltmarsh gradient.

Coastlines with no endemics either have little marsh habitat or have been subjected to heavy human disturbance. The lack of tidal-marsh endemics along the temperate Atlantic coastline of South America is probably the most difficult to explain, for despite the overall high species diversity of South American vertebrate faunas and the large number of species reported thus far from tidal marshes, we were unable to locate any endemic taxa associated with tidal marshes of the large estuaries of southeastern coast of the continent. Further research will confirm this pattern or determine that it is an artifact of less thorough collecting and less detailed taxonomic work at the subspecific level.

FUTURE RESEARCH

This paper is clearly a first assessment of diversity and endemism of terrestrial vertebrates in several of the tidal marsh systems throughout the world. For many taxonomic groups and for several regions there is a crucial need for basic inventory of species presence and absence. This would be particularly true for reptiles and amphibians outside of North America, birds and mammals in Asia, and all taxa in South Africa, and parts of the Middle East.

In groups for which alpha-level faunal lists are available or can be pieced together, a need remains for information focusing on more detailed distribution of taxa along a salinity and tidal gradient, together with complementary data on morphological and genetic variation between upland and tidal-marsh habitats.

We were able to piece together some information on the distribution and prevalence of tidal marshes. But for most regions it remains crude, particularly in comparison to the type of information that can be gathered and analyzed with remote-sensing technologies and geographic information system. A comprehensive review of different coastal-marsh types is an essential component to a more sophisticated analysis of marsh biogeography.

Although detailed information of recent and geologic history is available for certain estuarine and marsh systems, this information is scattered and is apparently not available for many coastlines. Much more information on the deep and recent history of coastal-marsh systems is also central to developing evolutionary and biogeographical hypotheses on the formation of tidal marsh assemblages.

Finally, the sharp environmental gradient between upland and freshwater habitats and saltmarsh is actually a composite of several selective gradients working in consort in shaping divergence in tidal marsh populations: salinity, geochemistry of the substrate and resulting coloration, and a shift to a more marine invertebrate prey base. Adaptations to any of these reinforce the selective advantage of assortative mating which leads to ecological- or physiologically based speciation. For these reasons, tidal marshes represent one of the best systems for studying ecological differentiation and speciation.

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