Southeast

The ecosystems of the Southeast range from the spruce–fir forests of the highest mountains east of the Mississippi River to the tropical hardwood hammocks of southernmost Florida. A tremendous diversity of ecosystems lies between these extremes: the sawgrass marshes, mangrove forests, and pine rockland of south Florida; the carnivorous plant wetlands, baldcypress swamps, live oak maritime forests, longleaf pine savannas, and dunes of the Coastal Plain; the oak–hickory forests, bottomland forests, prairies, glades, and barrens of the Piedmont and continental interior; the springs and extensive cave systems of limestone areas; and the old-growth deciduous and hemlock forests, cliffs, rocky stream gorges, and grassy and heath balds of the southern Appalachian Mountains.

Although broad-scale climatic patterns explain much of this diversity, the Southeast's most distinctive characteristic is diversity at small scales. Variation in topography determines soil moisture and temperature regime, influences soil fertility, and produces change in ecosystem composition and structure over relatively short distances. The Southeast is also underlain by a wide variety of geological substrates and soils; thus, where ecosystem boundaries are abrupt, a mosaic of community types results. Usually, however, changes in community types are gradual, and classification of community types itself becomes arbitrary. Many animal species move among and depend on the diverse aquatic and terrestrial habitats of southeastern landscapes.

In addition to environmental variation, there are other explanations for the Southeast's biological diversity. Historically, the Southeast was not covered by continental glaciers, nor was much of the present land surface submerged by past rises in sea level. As a result, plants and animals have evolved in the Southeast over long periods. This long evolution, combined with the isolation that characterizes some habitats, has produced striking levels of endemism (species restricted to certain habitats) in many groups of plants and animals. Narrowly restricted endemism is most prominent in groups with limited dispersal ability and those found in isolated habitats. For example, narrow endemism is frequent in plants, amphibians, fishes, mollusks, and aquatic insects in the Southeast but is weak in birds and mammals.

Because of diverse environments and long evolutionary isolation, a number of groups reach continental high points of species richness in the Southeast, making the region one of the richest areas in the temperate zone, surpassed only by eastern Asia (Hackney et al. 1992; Martin et al. 1993a,b). Groups that have their highest North American diversities in the Southeast include amphibians, fishes, mollusks, aquatic insects, and crayfishes throughout the region; salamanders, land snails, fungi, and plants in the southern Appalachians; and carnivorous plants on the Coastal Plain.

This chapter describes the status and trends of the rich biological diversity of the Southeast. The very diversity and local complexity of the region's ecosystems complicate our task. Long-term data are scarce and often are available for only a few study areas or taxonomic groups. The trends that are available are usually derived from expert opinion rather than extensive data sets and often concern loss of habitat area rather than change in populations or ecological processes (Noss et al. 1995). Our emphasis is on ecosystems because they are the best context for the consideration of biological diversity, but we also summarize status and trends for vertebrates and several other well-studied groups.

Environments of the Southeast

Landforms and Geology

The Southeast is divided into 4 physical divisions and 11 regions of distinctive landscapes (Isphording and Fitzpatrick 1992; Martin and Boyce 1993; Fig. 1). Bedrock consists of a variety of metamorphic, igneous, and sedimentary rocks that range greatly in chemistry and resistance to erosion and weathering. Acidic rocks are widespread in the Piedmont and mountains, but limestone and other basic rocks dominate in areas of the continental interior and much of peninsular Florida, and are scattered in other provinces.

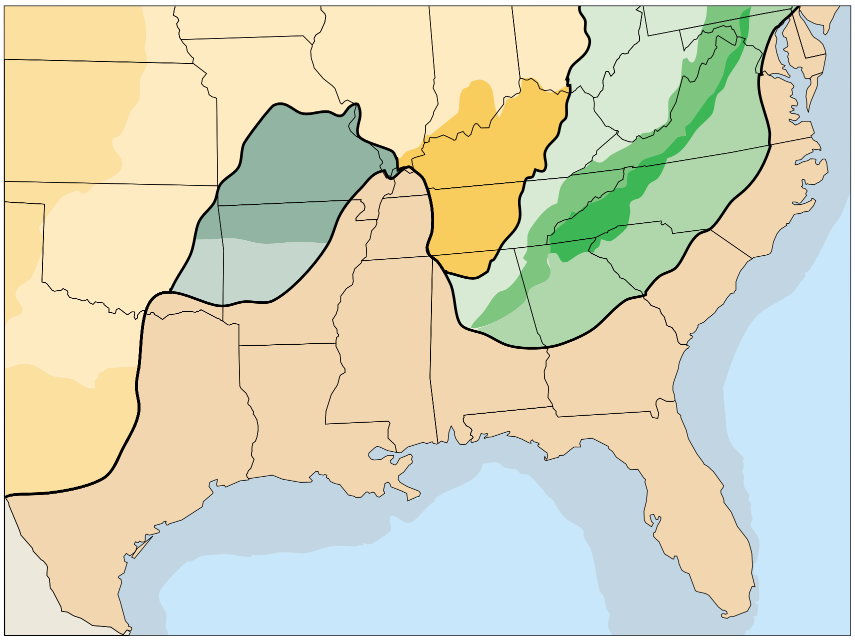


Fig. 1. Physiographic regions of the southeastern United States (redrawn from Martin and Boyce 1993).

The Coastal Plain includes the Atlantic Coastal Plain, the Gulf Coastal Plain, the Mississippi River valley (including the Mississippi Embayment that extends northward to Missouri and Kentucky), and peninsular Florida. Topographic relief is low, with maximum elevations reaching only 50–150 meters. An extensive system of barrier islands occurs along the Atlantic and Gulf coastal plains. Unconsolidated substrates in the Coastal Plain include peats, coarse sands, silts, acid clays, calcareous clays, loess, and shell hash.

Sand deposits in the Coastal Plain are derived from three sources (Christensen 1979). Marine sands occur on recently exposed terraces in a relatively narrow strip along the coast itself. Inland from the coast are aeolian sands, and yet farther inland and adjacent to the Fall Line (the border of the Piedmont and Coastal Plain) from North Carolina to Georgia are the Sandhills, a distinctive landscape of rolling hills (Christensen 1979). Elevations in the Sandhills are up to 100 meters higher than in adjacent areas, and the area's permeable sands make soils extremely dry despite high rainfall. Sandhill vegetation includes xeric oak and pine, pine savanna, and open herbaceous barrens. The driest places, in which vegetative cover is incomplete, are sometimes called *deserts*, an ironic title for a region with high rainfall.

The Appalachian Highlands include four parallel units: the Piedmont, Blue Ridge, Ridge and Valley, and Appalachian Plateaus. The Piedmont, with an elevation of 150–600 meters, is dominated by erosion-resistant metamorphic rock. The Blue Ridge encompasses the high peak region of the southern Appalachians, with the highest point in eastern North America on Mount Mitchell, North Carolina, at 2,037 meters. Erosion-resistant igneous and metamorphic rocks dominate the high elevations. The Ridge and Valley province, with elevations of 600–900 meters, consists of northeast–southwest trending valleys on limestone bedrock and intervening ridges of more resistant sandstones. The Appalachian Plateaus, with elevations of 600–900 meters, have areas with mountain peaks that rise above the plateau surface (though not reaching the height of the Blue Ridge) and other areas in which rivers have cut steep-sided valleys below the more gentle topography of the plateau surface.

The Interior Low Plateaus of central Tennessee, central and western Kentucky, and northern Alabama are part of the Interior Plains physical division. Limestone is a major influence on landforms, and karst features, such as extensive cave systems and sinkholes, are frequent. Relief is moderate, and elevation is about 300 meters.

The Ozark Plateaus and Ouachita Mountains of the Interior Highlands physical division dominate southern Missouri and northern Arkansas. Limestone, shale, and sandstone dominate these areas, and karst landforms are frequent.

Soils

All major soil orders are present in the region and are associated with particular landforms and geographic areas. Soils vary greatly in texture, fertility, and moisture-holding capacity (Hackney and Adams 1992; Martin and Boyce 1993). Ultisols dominate the upland soils of the Southeast, underlying about three-quarters of the area (Martin and Boyce 1993). Upland ultisols (udults) are developed on deeply weathered parent material and are acidic and leached. Long agricultural use has reduced organic matter content in many areas. Aquults (a waterlogged soil) occur in wetter areas on unconsolidated sediments, especially along the Atlantic Coastal Plain.

Climate

Southeastern climates are humid and warm-temperate to subtropical. Major variation in climate occurs with change in latitude and elevation. Longitude has a more subtle influence on climate than latitude, as a result of maritime influence to the south and east and continental influences to the north and west.

Latitudinal gradients in temperature are steeper in winter than in summer, producing a strong geographic pattern in freeze-free periods and cold temperatures. The gradient in average minimum January temperature spans 22°C, whereas the gradient in average maximum July temperature spans only 4°C (Ruffner 1985; Martin and Boyce 1993; Table 1). The freeze-free period decreases northward, from 365 days in the Florida Keys, which experienced freezing temperatures in fewer than half of the years on record, to 180 days in Arkansas and 150 days in northern Virginia. The freeze-free period also decreases with elevation, to 110 days at the highest elevations in the southern Appalachians. Canadian air masses bring the coldest winter temperatures, penetrating the Southeast from the continental interior and generally producing decreasing minimum temperatures westward at a given latitude. Annual snowfall shows the same steep gradients as cold winter temperatures, increasing from zero in south Florida to over 100 centimeters northward and to over 200 centimeters in the high mountains.

Annual precipitation averages 110–140 centimeters over much of the area, with a slight decrease northward to about 100 centimeters. Excluding the high mountains, the highest annual precipitation occurs along the Gulf of Mexico coast and in south Florida (140–160 centimeters). Annual precipitation increases to 200 centimeters where elevations surpass about 1,700 meters. The highest values are not, however, at the extreme elevations but are affected by the position of the mountain front relative to precipitation sources. The first high mountains encountered by moist air masses from the Gulf of Mexico coast and the Atlantic are those at the southern edge of the Blue Ridge near the joint boundaries of the region of North Carolina, South Carolina, and Georgia. This region has the Southeast's highest precipitation (as much as 250 centimeters) and the highest rainfall in the United States east of the Pacific Northwest.

Precipitation occurs throughout the year but is generally lowest in fall and highest in summer, when convective thunderstorms develop. Thunderstorms in Florida occur an average of 80–130 days annually, in the Gulf Coastal Plain 80–100 days annually; the number of thunderstorms decreases northward, occurring an average of 40–60 days a year in Kentucky, Virginia, and interior regions.

By combining climate and physiography, McNab and Avers (1994) classified the Southeast into 2 domains (humid temperate and tropical), 3 divisions (humid temperate, hot continental; humid temperate, subtropical; and humid tropical, savanna), 9 provinces, and 28 sections, the latter representing distinctive landscape types (Table 2).

Table 1. Climates of the Southeast (from Ruffner 1985).

Location	Mean temperature (°C)				Mean annual precipitation		Relative humidty (%)
	January		July		Rain (cm)	Snow (cm)	
	Low	High	Low	High			
Elkins, West Virginia	-7	5	14	27	109	170	50
Baltimore, Maryland	-4	6	19	31	102	56	66
Louisville, Kentucky	-4	6	19	31	109	43	70
Little Rock, Arkansas	-2	10	21	34	125	13	71
Asheville, North Carolina	-3	9	17	29	114	46	75
Richmond, Virginia	-2	8	20	31	109	36	68
Memphis, Tennessee	0	9	22	33	125	15	69
Atlanta, Georgia	1	11	21	31	122	4	70
New Orleans, Louisiana	7	17	23	32	145	0.5	76
Miami, Florida	15	24	24	32	152	0	73

Table 2. Landscape diversity in the Southeast: ecological subregions of the southeastern United States as mapped by the U.S. Forest Service (McNab and Avers 1994), based on Bailey's ecoregions.

Domain	Division	Province	Number of	
			Sections	Vegetation types[a]
Humid temperate	Hot continental	Eastern broadleaf forest–oceanic	4	5
		Eastern broadleaf forest–continental	3	6
		Central Appalachian broadleaf forest–coniferous forest–meadow	3	6
		Ozark broadleaf forest–meadow	1	2
	Subtropical	Southeastern mixed forest	7	7
		Ouachita mixed forest–meadow	1	1
		Outer Coastal Plain mixed forest	7	7
		Lower Mississippi riverine forest	1	2
Humid tropical	Savannah	Everglades	1	5

[a]Küchler (1964). See Table 3 for Küchler vegetation types.

Natural Disturbances

The Southeast's frequent thunderstorms provide an ignition source for natural fires. In the past, Native Americans and European settlers also burned natural vegetation regularly. Regardless of ignition source, fire frequency and intensity have been dominant forces throughout the Southeast on all but the wettest and coldest (high mountain) sites. The mid- to late 1900's represent a period of reduced fire frequency, size, and intensity, a shift that is a major source of change in the region's ecosystems, leading to increases in mesic species (that is, species adapted to moister conditions), increased understory stem density, increased woody cover in formerly open habitats, and decreases in fire-dependent species and ecosystems.

Tropical storms are also a major recurrent disturbance, with much of the area experiencing about two damaging storms per decade. Between 1871 and 1981, 138 tropical storms affected south Florida (Davis and Ogden 1994a). Although storm incidence declines from coastlines to the interior, tornadoes are more frequent in interior areas, where nearly 10 violent tornadoes per year have occurred over the last 100 years (Grazulis 1984; Martin and Boyce 1993).

The heavy rainfall that accompanies these and less violent storms is an important natural disturbance, especially in the Appalachian Mountains, where debris avalanches create open habitats in the forested matrix and flash floods scour stream banks and affect stream biota. Throughout the Southeast, the natural flooding and erosional dynamics of rivers were and are an important natural process for biological diversity; impoundments, changes in the quality and quantity of water, draining of bottomlands, and channelization of rivers are major causes of loss in the biological diversity dependent on dynamic stream and river systems.

Evolutionary History

Although consideration of environmental variation is one key to understanding the Southeast's biological diversity, a deeper look at the pattern reveals a second major explanation, one based on evolutionary history and geography. Because some habitats in the Southeast have long been isolated from one another, evolution could produce a geographic turnover of species with restricted distributions. This phenomenon is most striking in the biota of rivers and streams and in groups with low dispersal abilities. For example, aquatic taxa evolved in relative isolation in river basins, with interchange made possible at rare intervals by stream capture or by rare dispersal events. This phenomenon has given a geographic pattern to the distribution of freshwater fishes and mollusks (Sheldon 1988; Walsh et al. 1995). A terrestrial example of the evolution of endemism in isolated areas is provided by Lake Wales ridge, an area of Florida that has been continuously above sea level for 3 million years (Martin 1993).

Even though the Southeast was not glaciated, changing climates did result in the migration of plant and animal populations over considerable distances, with some terrestrial species becoming restricted to isolated refugia (Delcourt et al. 1993). This historical fragmentation of range for some taxa allowed further opportunity for separate evolution. In addition, some species never rebounded from glacial refuges.

These mechanisms enriched the Southeast in its number of local endemics. For example, some of the continent's rarest woody plants are found in a series of river valleys in south Georgia and northern Florida: Florida torreya (now in a 35-year decline, with no sexual reproduction having occurred in the last 15 years [Schwartz and Hermann 1993, 1995]), Florida yew, and Franklinia, last seen in the wild in the early 1800's but widely grown in gardens. In the southern Appalachians, an imprint of evolutionary history can also be seen in plants (for example, Rugel's ragwort is limited to but abundant in the Great Smoky Mountains) and animals (for example, salamanders) that are limited to particular parts of the mountains. The presence of local endemics further complicates our overview of biodiversity trends in the Southeast because it means that the species composition of a particular kind of ecosystem may vary from one place to another—and this variation often involves the very species (local endemics) that are most at risk.

Human Populations and Land Use

Native Americans have occupied the Southeast for more than 10,000 years, but their influence on ecosystems and species varied considerably through time (Delcourt et al. 1993). Shifting agriculture on bottomlands and alluvial terraces became dominant during the Woodland Period (3,000 to 1,200 years B.P.). The wide use of maize as a staple crop plant marked the period of maximum cultivation in the Mississippian Period (1,200 to 500 years B.P.). In this period, productive floodplains and lower river terraces were extensively cleared and large settlements were created whose influence included the harvest of wood for fuel and building materials in peripheral areas (Delcourt et al. 1993). Native American populations declined sharply after 1500 because of the spread of European diseases and displacement by European settlers.

European settlement, including its concomitant and ubiquitous introduction of livestock and new crop plants, resulted in more extensive conversion of upland forests to agriculture. The time of maximum clearing varied across the Southeast, but for many areas the peak occurred in the mid-nineteenth to the early twentieth century. Old-growth forests that survived this period were almost always on less productive or hard-to-cultivate land. Although logging took place throughout the region from the earliest settlement times to the present, mechanized logging was particularly destructive in the southern Appalachians between about 1880 and 1920. Soil erosion is a problem on farmed and logged sites and may have permanently reduced productivity over large areas. In addition, soil erosion produced a heavy sediment load in aquatic systems; this load has only recently begun to decrease (Mulholland and Lenat 1992).

Because human influences have changed over the last century, upland forests are undergoing successional change over much of the Southeast. Skeen et al. (1993) argue that pine-forest cover in the region peaked in about 1965. Since then, forest cover has declined because of the reductions in fire frequency that began about 1900 and because of the senescence of old-field pine that had colonized farms that were abandoned in the mid- and late nineteenth century.

After a peak in cleared land in the mid-nineteenth to early twentieth century, a major period of farm abandonment occurred, starting about the time of the Civil War and continuing until about 1940. These old fields were invaded by pines; some patches of shorter-lived pine species, such as short-leaf pine and Virginia pine, which live 80–120 years, are now senescing (Skeen et al. 1993).

For pine stands that originated through fire or farm abandonment, a native insect, the southern pine beetle, is often the immediate agent of death. Outbreaks of this insect are more common in older and stressed trees. Human activities may have resulted in larger blocks of pine forest of relatively uniform age, producing landscapes more susceptible to large outbreaks of this beetle. Although these outbreaks can be alarming and can render trees hazardous to human life and property, the southern pine beetle is a native species that may play a role in natural fire regimes by helping produce heavy fuel loads (White 1987).

Understanding fragmentation effects and managing for tracts of unbroken forest in the midst of growing human populations have become critical issues. For example, the persistence of common forest interior bird species such as the wood thrush requires a minimum of 40 to 100 hectares (Robbins et al. 1989); some species, though, such as the ivory-billed woodpecker (extirpated in the Southeast but perhaps surviving in Cuba), require 2,000 to 40,000 hectares to achieve status as a source population (that is, a long-persisting population that has excess production for colonizing new areas [W. C. Hunter, U.S. Fish and Wildlife Service, Atlanta, Georgia, unpublished report]). Fragmentation of forests will be a dominant issue in conservation of biological diversity across the Southeast during the coming decades.

Destructive logging and soil erosion in the Southeast were major stimuli to the conservation movement in the early twentieth century; this movement led to the creation of national forests, national parks, state parks, research stations, and other protected areas. In contrast to the western United States, the Southeast had little public land—less than 10%—and these areas had to be created by purchase of private lands. Today, public land is mostly in the mountains, with less public land in the Piedmont and Coastal Plain (Boyce and Martin 1993; Fig. 2).

The Southeast has one of the country's most rapidly growing human populations. Population growth was 20% from 1970 to 1980, 13.4% from 1980 to 1990, and an estimated 10%–19% for the 1990's (U.S. Bureau of the Census 1994). The continued growth of the human population and changes in the way humans interact with the natural landscape present a challenge to conservationists concerned with the survival of diversity in this biologically rich region.

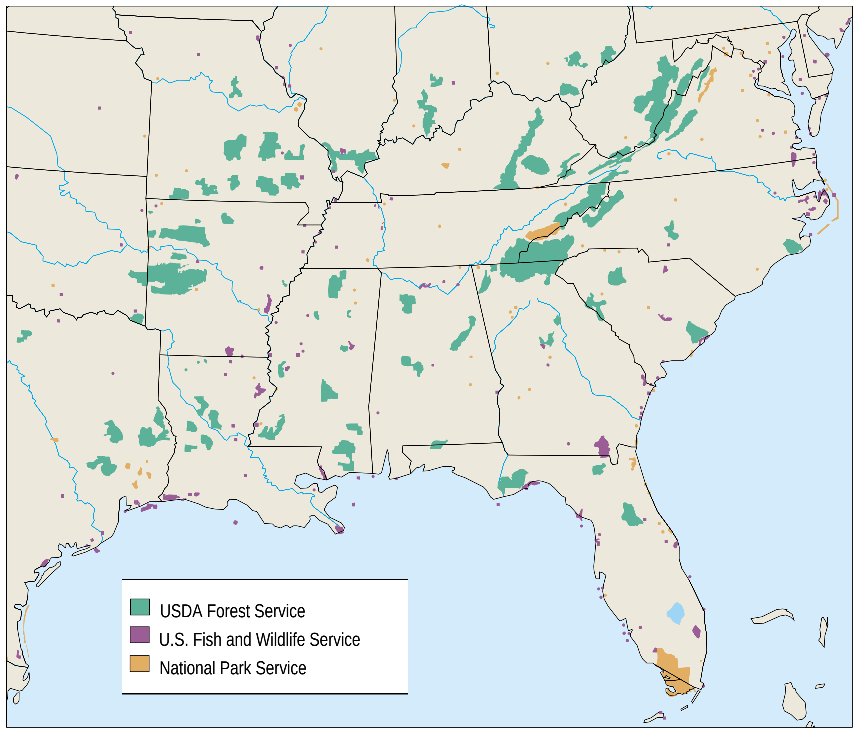


Fig. 2. Distribution of federal land in the southeastern United States, including national parks, forests, and wildlife refuges of significant area. The Southeast has little public land in comparison to the western United States.

Land-Use Trends

Data from 1987 show that although 55% of the land was forested then, the trend was downward, with a decline of 5% since 1960 (U.S. Forest Service 1988; Martin and Boyce 1993). The rest of the land was used for crop and pasture (31%) and miscellaneous purposes (roads, towns, cities, airports; 14%). Urban areas are growing at the fastest rate, but the rate of growth varies by region. For example, in North Carolina, urbanization occurred three times faster in the Piedmont than in either the mountains or Coastal Plain (see review in Boyce and Martin 1993). While the high total of forested land indicates potential for the survival of biological diversity, these forests are largely privately owned (less than 10% of the forested land is in federal ownership [U.S. Forest Service 1988]) and are not managed for biological diversity per se. Further, because these lands have almost all been disturbed by logging and agriculture, they have already lost communities and species.

Forestland has been predicted to decline by 15% over the next 50 years (with additional forestland converted from natural to plantation forests), agricultural land to decline slightly (with a continued shift from small to large farming operations), and urban areas to increase in area (see discussion in Boyce and Martin 1993), suggesting that further habitat loss and fragmentation will occur near human population centers. We know too little about the survival of biological diversity in human-dominated landscapes, but we do know that the biodiversity of these areas will generally decrease with habitat fragmentation (Harris 1984). Some human-dominated landscapes, however, have the potential to support the diversity of some groups. For example, some crop systems support bird diversity (Allen 1995; Hunter, draft report) by cultivating marginal lands, including some wetlands.

Ecosystem Diversity

The natural landscape of the Southeast is dominated by broad-leaved deciduous trees and pines (Bryant et al. 1993; Skeen et. al. 1993; Stephenson et al. 1993). On uplands, a compositional continuum occurs from mesic sites dominated by maples, American beech, and other species to drier upper slopes and ridges dominated by oaks, hickories, and pines. Except for pines and eastern redcedar (widely distributed in the Southeast, particularly on calcium-rich soils), other gymnosperms are more restricted in distribution. Hemlock, spruce, and fir are found only in the southern Appalachian Mountains, with Atlantic white-cedar and baldcypress limited to the Coastal Plain. Broad-leaved evergreen trees, including southern magnolia and live oak, are prominent in some Coastal Plain habitats. Tropical hardwoods are limited to south Florida and are unique in the continental United States.

Most southeastern forests are closed-crowned, but savanna occurs on dry and fire-affected sites. Historically, longleaf pine savanna was widely dominant on the Coastal Plain; oak savanna was important on the margin of prairies in the continental interior. Open habitats, including fens, bogs, glades, barrens, and prairies; freshwater and saline marshes; sand dunes; and salt flats and rock outcrops form islandlike habitats within the matrix of closed forest. The occurrence of such open communities is variously explained by frequent fires, thin soils, unusual soil chemistry, or flooding.

How many kinds of ecosystems occur in the Southeast? What are the distributions and extents of these ecosystems? Unfortunately, we cannot answer these questions with much precision, although The Nature Conservancy (Grossman et al. 1994; The Nature Conservancy and Environmental Systems Research Institute 1994), in cooperation with State Heritage programs and the U.S. Geological Survey, has embarked on a long-term project to fill this gap in our knowledge. Although the lack of data on the definition and distribution of ecosystem types is a problem throughout the United States, the local complexity of southeastern ecosystems makes the problem particularly severe.

We have chosen to outline ecosystem diversity in the Southeast at two scales. First, for relatively coarse scales, we will summarize Küchler's (1964; McNab and Avers 1994) map of potential natural vegetation, a work also used as a starting point in Hackney et al. (1992) and Martin et al. (1993a,b). For relatively fine scales, we will use The Nature Conservancy's national classification scheme (The Nature Conservancy and Environmental Systems Research Institute 1994).

Regional Ecosystem Diversity: Coarse Scale

Küchler (1964) mapped 24 potential natural vegetation types in the Southeast (map scale, 1:3,168,000), of which 12 were forest types (Table 3). Six types were widely distributed, 3 were restricted to the Appalachian Mountains, and 13 were restricted to the Coastal Plain, with 7 of those restricted to Florida (Table 3). The final 2 types are cedar glades (restricted to the continental interior and generally found on dry sites over calcium-rich bedrock) and rock outcrops (scattered throughout).

The coarse scale of the Küchler types is evident in a recent treatment of the Southeast (Martin et al. 1993b). For example, in Florida, Küchler mapped 2 communities in the Everglades, whereas Gunderson and Loftus (1993) described 13; Küchler mapped 1 mangrove community, whereas Gilmore and Snedaker (1993) described 5; and Küchler mapped 2 pine communities, whereas Stout and Marion (1993) described 5.

Regional Ecosystem Diversity: Fine Scale

The Nature Conservancy's national classification (The Nature Conservancy and Environmental Systems Research Institute 1994) includes 7 hierarchical levels, the first 5 of which are determined by noncompositional factors: system (terrestrial, aquatic, or subterranean), physiognomy (growth form, height, phenology, and cover of the strata), and

Table 3. The distribution of the 24 Küchler (1964) types of potential natural vegetation mapped in the Southeast.

Küchler type	Distribution in the Southeast
Widely distributed, upland forests	
Southern mixed	Virginia, North Carolina, South Carolina, Georgia, Alabama, Mississippi, Louisiana, Texas, Florida
Oak–hickory–pine	Virginia, North Carolina, South Carolina, Georgia, Alabama, Mississippi, Louisiana, Arkansas, Texas
Oak–hickory	Arkansas, Kentucky, Tennessee, Alabama, Mississippi
Appalachian oak	West Virginia, Maryland, Virginia, Tennessee, North Carolina, South Carolina, Georgia, Kentucky
Mixed mesophytic	West Virginia, Kentucky, Tennessee, Alabama
Widely distributed, wetland forest	
Southern floodplain forest	Throughout the Southeast
Restricted, mountain forests	
Northeastern spruce–fir	High mountains only: West Virginia, Virginia
Southeastern spruce–fir	High mountains only: Virginia, Tennessee, North Carolina
Northern hardwoods	Mountains only: West Virginia, Virginia, Tennessee, North Carolina, Georgia
Restricted, Coastal Plain vegetation	
Live oak–sea oats	Coastal Plain: North Carolina to Alabama
Pocosin	Coastal Plain: Virginia to South Carolina
Northern cordgrass prairie	Coastal Plain: Virginia, North Carolina
Restricted, Florida	
Mangrove forest	Coastal Plain: south Florida
Marl Everglades	Coastal Plain: south Florida
Everglades	Coastal Plain: south Florida
Subtropical pine forest	Coastal Plain: south Florida
Cypress savannah	Coastal Plain: south Florida
Sand pine scrub	Coastal Plain: Florida
Palmetto prairie	Coastal Plain: Florida
Other restricted types	
Cedar glades	Various sections: Tennessee, Alabama, Missouri, Arkansas
Blackbelt	Coastal Plain: Alabama, Mississippi
Bluestem–sachuista prairie	Coastal Plain: Texas, Louisiana
Southern cordgrass prairie	Coastal Plain: Texas, Louisiana
Rock outcrops	Scattered throughout the Southeast

environmental factors (including heat, moisture, seasonality, and dynamics. The lowest two levels, alliance and community elements, are based on plant composition. The Nature Conservancy's draft scheme for its terrestrial system constitutes a rough index of ecosystem variation in the Southeast (Table 4). The scheme includes 480 alliances and 629 community elements (The Nature Conservancy and Environmental Systems Research Institute 1994). Over one-half (274) of the alliances are in the forest or woodland physiognomic class (versus 13 forest vegetation types in Küchler 1964; Table 3).

These large numbers of alliances and elements partly reflect the difficulty of classifying the Southeast's plant communities. Southeastern landscapes have mosaiclike arrangements of contrasting ecosystems and continuous variation between obvious extremes. Past disturbances, particularly fire, also have influenced ecosystem composition and boundaries. Even though the draft classification is an index to structural and compositional diversity, more work remains to be done.

Table 4. The Nature Conservancy's classification of structural and compositional variation in vegetation: the terrestrial system in the Southeast (Grossman et al. 1994; The Nature Conservancy and Environmental Systems Research Institute 1994).

Physiognomic class	Physiognomic subclass	Number of			
		Formation groups	Formations	Alliances	Community elements
Forest					
	Evergreen	4	12	72	99
	Deciduous	1	6	77	120
	Mixed	2	6	44	54
Woodland					
	Evergreen	2	8	46	77
	Deciduous	1	3	21	25
	Mixed	1	2	4	20
Sparse woodland					
	Evergreen	4	7	16	19
	Deciduous	2	8	16	16
	Mixed	1	4	5	5
Shrubland					
	Evergreen	3	7	31	36
	Deciduous	1	5	19	19
	Mixed	1	3	5	5
Sparse shrub					
	Evergreen	2	4	10	12
	Deciduous	1	2	3	3
Dwarf shrubland					
	Evergreen	1	2	4	4
	Deciduous	1	1	1	1
Sparse dwarf shrubland					
	Evergreen	1	3	3	3
Herbaceous					
	Tall grassland	2	10	32	40
	Medium-tall grassland	1	5	17	22
	Short grassland	1	5	7	7
	Tall forb	1	3	6	6
	Low forb	2	5	8	8
	Hydromorphic	2	3	12	16
Miscellaneous					
	Cliffs	1	2	5	5
	Saltwater	2	3	6	7

Rare, Endangered, and Threatened Ecosystems

Grossman et al. (1994) used The Nature Conservancy classification to produce the first list of rare plant communities in the United States. Global ranks ("G" ranks) were assigned to each type of plant community based on the number of occurrences, areal extent, trends in areal extent, condition, threats, and fragility. Excluding Texas and Oklahoma (which are in The Nature Conservancy's Southeast Region, but which include many midwestern and western ecosystem types), there are 58 plant communities found throughout the Southeast that have global ranks of G1 or G2, of which 44 are endemic to this region. (G1 = most endangered; found in 1–5 occurrences globally. G2 = found in 6–20 occurrences globally; if found in 21–100 occurrrences, then found on fewer than 4,047 hectares total.) Twenty-one types occur in the Coastal Plain (excluding south Florida), 5 in south Florida, 17 in the southern Appalachian Mountains, and 11 in the continental interior (Table 5). Major threats to these communities are invasions by nonindigenous species, development, hydrological alteration, fire suppression, recreation, grazing, agricultural conversion, and fragmentation (Table 5).

Table 5. Summary of distributions and threats for The Nature Conservancy's 57 rare plant communities of the Southeast (after Grossman et al. 1994).

Geographic area	Habitat	Number of communities	Threats (number of community types)
Southern Appalachian Mountains	Spruce–fir	2	Nonindigenous species (5), recreation (4), air pollution (3), past logging (2), hydrological alteration (2), succession (1)
	Beech	2	
	Bog, fen	7	
	Grassy bald	1	
	Cliff, gorge	4	
	Other	1	
South Florida	Tropical hardwood	2	Development (4), nonindigenous species (4), hydrological alteration (2), fire suppression (2), burning (2), fragmentation (1), agriculture (1), recreation (1)
	Slash pine	3	
Coastal Plain	Barrier island	9	Development (9), grazing (7), fragmentation (6), hydrological alteration (5), fire suppression (5), nonindigenous species (5), agriculture (3), logging (3), mining (2), burning (2), recreation (2)
	Longleaf pine	3	
	Other forests	3	
	Glade, prairie	6	
Continental interior	Forest	7	Fire suppression (3), agriculture (3), recreation (2), grazing (2), logging (1), nonindigenous species (1), succession (1), mining (1), hydrological alteration (1)
	Glade, prairie	3	
	Other	1	
Other	Outcrop	1	Recreation (1), grazing (1), agriculture (1), hydrological alteration (1), fire suppression (1)
	Forest	1	
	Canebrake	1	

Noss et al. (1995) based their work on information sources similar to those used by Grossman et al. (1994), namely a survey of the State Heritage programs, but they also surveyed other researchers and reviewed published works. Unlike Grossman et al. (1994), Noss et al. (1995) did not attempt a hierarchical classification or a standard definition of types; thus, their ecosystem types are more generalized. The importance of the assessment by Noss et al. (1995) lies in its summary of trends in habitat loss and fragmentation. Our own review and discussion will follow the Noss et al. (1995) list closely.

If we allow for the broader definition of types in Noss et al. (1995), all of the 57 rare plant communities of Grossman et al. (1994) appear in the top categories of percentage loss (Table 5 versus Table 6). There are three ecosystems listed by Noss et al. (1995) but not by Grossman et al. (1994): old-growth deciduous forest (in the top category of endangerment), Atlantic white-cedar (listed because of habitat loss in two states rather than rangewide habitat loss), and cedar glades (listed because of habitat loss in one state). The lack of listing of old-growth forest by Grossman et al. (1994) pointed out that The Nature Conservancy's draft classification hierarchy does not include an important aspect of biological diversity conservation: an undisturbed remnant of a given community type may not differ in structure (closed forest) or dominance (the major variable for definition of alliances is canopy composition) from a second-growth forest and yet may possess intact soils and associated biological diversity (for example, understory herbs, soil biota, amphibians) that are absent from disturbed sites (Meier et al. 1995).

Noss et al. (1995) reported 50 endangered and threatened ecosystems in the Southeast: 14 critically endangered ecosystems (greater than 98% loss), 25 endangered ecosystems (85%–98% loss), and 11 threatened ecosystems (70%–84% loss). An additional 24 communities were reported as having at least 50% loss of area (Table 6). Major themes of loss on the Noss et al. (1995) list are as follows: old-growth forest because of logging, agriculture, and development (Tables 6 and 7); wetlands and bottomland forests because of hydrological alteration and conversion to agriculture (Tables 6 and 7); spruce–fir forests because of logging, an exotic insect invasion, and air pollution; longleaf pine and other pine ecosystems because of fire suppression and conversion to plantation forestry; prairies and glades because of grazing, development, fire suppression, and conversion to agriculture; Atlantic white-cedar because of logging and hydrological alteration; and maritime forests and other coastal communities because of development. Whether on private or public land, pristine areas and rare habitats in the Southeast have suffered heavy losses (Hackney et al. 1992; Martin et al. 1993a,b; Grossman et al. 1994; Noss et al. 1995). Further, human effects have permeated the region, rather than encroaching into the region along one or even several fronts.

Regionwide Themes of Change

As the previous overview indicates, changes in southeastern ecosystems include three major regionwide trends: loss of old-growth forest and pristine habitats in general, reduction in the importance of fire, and alterations to natural hydrology. We will further define these themes of change before discussing individual ecosystem types.

Table 6. Estimates of ecosystem loss from Appendix A of Noss et al. (1995), compiled from published papers, State Natural Heritage programs, The Nature Conservancy, and expert opinions. Ecosystems are listed in declining order of percentage loss. As discussed in detail in Noss et al. (1995), some estimates are based on more quantitative analysis than others, and not all states had data to report.

Ecosystem type	Geographic area
>98% loss: critically endangered	
Old-growth deciduous forests	Southeast
Southern Appalachian spruce–fir	Tennessee, North Carolina, Virginia
Longleaf pine	Coastal Plain
Rockland slash pine	Florida
Loblolly–short-leaf pine	West Gulf Coastal Plain
Canebrakes	Southeast
Bluegrass–savannah–woodland	Kentucky
Blackbelt prairie, Jackson prairie	Alabama, Mississippi
Dry prairie	Florida
Wet and mesic coastal prairies	Louisiana
Atlantic white-cedar	Virginia, North Carolina
Native prairies	Kentucky
Bottomland forest	West Virginia
High-quality oak–hickory	Cumberland Plateau, Tennessee
85%–98% loss: endangered	
Mesic limestone forest	Maryland
Red spruce	Central Appalachians
Spruce–fir forest	West Virginia
Upland hardwoods	Coastal Plain, Tennessee
Old-growth oak–hickory	Tennessee
Cedar glades	Tennessee
Longleaf pine	Texas, Louisiana
Longleaf pine forest, 1936–1987	Florida
Mississippi terrace prairie, calcareous prairie, Fleming glades	Louisiana
Live oak, live oak–hackberry	Louisiana
Prairie terrace–loess oak forest	Louisiana
Mature forest, all types	Louisiana
Short-leaf pine–oak–hickory	Louisiana
Mixed hardwood–loblolly pine	Louisiana
Xeric sandhill	Louisiana
Stream terrace–sandy woodland–savannah	Louisiana
Slash pine, 1900–1989	Florida
Gulf coast pitcher-plant bogs	Coastal Plain
Pocosins	Virginia
Mountain bogs	North Carolina
Appalachian bogs	Blue Ridge, Tennessee
Upland wetlands	Highland Rim, Tennessee
Aquatic mussel beds	Tennessee
Natural barrier island beaches	Maryland
Ultramafic glades	Virginia
70%–84% loss: threatened	
Bottomland and riparian forest	Southeast
Xeric scrub, scrubby flatwoods, sandhills	Lake Wales ridge, Florida
Tropical hardwood hammock	Florida Keys
Saline prairie	Louisiana
Upland longleaf pine	Louisiana
Live oak–pine–magnolia	Louisiana
Spruce pine–hardwood flatwoods	Louisiana
Xeric sandhill woodlands	Louisiana
Flatwood ponds	Louisiana
Slash pine–pondcypress–hardwood	Louisiana
Wet hardwood–loblolly pine	Louisiana
60%–70% loss	
Pocosins	Southeast Coastal Plain
Pocosins, 1952–1979	North Carolina
Sand pine	Florida
Baldcypress–tupelo	Mississippi, Tennessee
Mixed mesophytic forest	Cumberland Plateau, Tennessee
Bottomland forest	Tennessee
Oak–hickory forest area	Cumberland Plateau, Tennessee
Flatwoods–swale habitats	Florida
50%–60% loss	
Bottomland hardwood and baldcypress, 1900–1978	Southeast
Herbaceous marsh	Florida
Southern mesophytic forest	Louisiana
Calcareous forest	Louisiana
Hardwood slope forest	Louisiana
Freshwater marsh, interior saline marsh, interior salt flat	Louisiana
Scrub–shrub swamp	Louisiana
Baldcypress–tupelo swamp	Louisiana
Bayhead swamp	Louisiana
Small stream forest	Louisiana
Bottomland hardwoods	Louisiana
Cove hardwood forest	Blue Ridge, Tennessee
Barrier island dunes	Maryland
Coastal Plain seasonal ponds	Maryland
Cedar glade area	Tennessee
Cedar woodlands	Louisiana

Loss of Upland Old-Growth Forests

The Southeast's forests have overlapped broadly with intense human activities from Native American times to the present. Even though forests now make up 55% of the land in the Southeast, nearly all forests are second-growth, and many sites experienced soil erosion and loss of fertility during logging and agricultural use. Some logged lands have been converted to plantation forestry, a practice that results in low-diversity pine stands. Even surviving old-growth forests have experienced human-caused changes, including the loss of large grazing animals (for example, woodland bison and eastern elk), the loss of predators (for example, red wolves, gray wolves, and mountain lions), periods of understory livestock grazing (including by feral pigs), recent increases in white-tailed deer populations, invasions by nonindigenous species, and reductions in fire frequency. Some nonindigenous species have caused many adverse effects, (including wild boar in the mountains and feral pigs in the Coastal Plain, horses on some barrier islands, chestnut blight in the oak–chestnut forests of

Table 7. Percentage losses of forest and wetland by geographic area. Wetland losses from Noss et al. (1995) and Dahl (1990). Losses of old-growth forest and forest area from Noss et al. (1995). Data for specific wetland types are listed in Table 6.

Geographic area	Description	Loss (percent)
Alabama	Wetlands 1780–1980	50–60
Arkansas	Wetlands	70–84
Florida	Wetlands	25–50
	Original forest 1940–1980	27
Georgia	Wetlands	20–25
Piedmont	Original forest	70–84
Kentucky	Wetlands 1780–1980	70–84
	Old-growth forest	>98
Louisiana	Wetlands 1780–1980	25–50
Tensas Basin	Forested wetlands, since 1937	85
Mississippi	Wetlands 1780–1980	50–60
Maryland	Wetlands 1780–1980	70–84
North Carolina	Wetlands 1780–1980	25–50
South Carolina	Wetlands 1780–1980	25–50
Southeast Coastal Plain	Presettlement wetlands, 1986	25–50
Tennessee	Wetlands 1780–1980	50–60
Blue Ridge	Old-growth forest	85–98
Cumberland Plateau	Old-growth forest	85–98
Highland Rim	Upland wetlands	85
Texas	Wetlands 1780–1980	50–60
Big Thicket	Old-growth forest since 1960	85–98
Virginia	Wetlands 1780–1980	25–50
West Virginia	Wetlands 1780–1980	20–25

Texas Natural History: A Century of Change

The conservation of Texas's diverse and unique biota depends on reliable data about the flora and fauna of the region before it was negatively affected by humans. The recent discovery of the original files of a historical biological survey (conducted by the federal government from 1889 to 1906) gives a virtual natural history picture of every region of the state as it existed a century ago. This information provides crucial baseline data to compare with the results of current biological surveys and to assess landscape and biotic change information useful to land managers and others seeking to improve land and ecosystem management.

Texas was very different at the turn of this century; in 1900, the human population was fewer than 3 million, compared with about 17 million people today, and at the turn of the century more than 80% of the population was rural, compared with fewer than 20% today. Agriculture and ranching were the primary occupations then, whereas today the state is much more urbanized and industrialized.

Besides the biological diversity of Texas land, its other most significant characteristic is that about 97% of the land area is in private ownership, which is a major factor in biological resource management. Unlike other states, Texas entered the Union as an independent nation and retained its private lands, which were sold to pay indebtedness, build the government, and endow public schools.

The Biological Survey of Texas

Toward the end of the 1800's, the United States government established a new government program to inventory wildlife and assess its practical value. C. Hart Merriam was selected in 1885 to head this new division of the U.S. Department of Agriculture, called the U.S. Biological Survey (Sterling 1989). Merriam picked a series of states, including Texas, for intensive biological survey and inventory. Over about a 20-year period (1889–1906), a team of 12 scientists and field agents led by Vernon Bailey extensively surveyed the state. Bailey's most famous collaborator was ornithologist Harry C. Oberholser, who prepared the bird report. Bailey prepared the mammalian component and assembled the more incidental accounts of reptiles.

In Texas, the federal field agents worked an equivalent of more than 5 years of continuous fieldwork. They prepared written reports describing the state's physiography and plants and listing the birds and mammals they observed or captured at 178 different sites in all 10 ecological regions of the state. Many of these sites have changed dramatically.

The field agents devoted much work to mapping life zones and documenting agricultural crops and pests. They equated life zones with crop zones to help predict new crops that might be grown in the state; this was the practical part of the survey. Merriam, who believed that temperature was the predominant factor governing the distribution of plants and animals, divided Texas into three life zones: the lower austral zone, with a humid austroriparian region, its gulf coastal strip, and the more arid lower Sonoran divisions; the upper austral zone of the Staked Plains and the foothills of the western mountains; and the transition zone, which was restricted to the Chisos, Davis, and Guadalupe mountains above 1,850 meters in the Trans–Pecos region. The field agents developed a detailed map of these life zones and took more than 1,000 black-and-white photographs of Texas landscapes, habitats, plants, and animals. In addition, the agents developed numerous maps of plant and animal species and their distributions.

Bailey and the field agents relied heavily on local naturalists and landowners while conducting the survey. Bailey particularly relied on an Englishman named Howard Lacey, who owned a ranch near Kerrville in the Hill Country of central Texas. Bailey visited Lacey's Ranch (Fig. 1) on several occasions, and he named a new subspecies of mouse after Lacey from specimens he collected there.

Local residents contributed much to the wildlife information base in the historical survey. For example, Ab Carter, a farmer from the Big Thicket region in the southeastern part of the state, provided Bailey with information about the demise of bear populations in this area. According to Carter (Fig. 2), he and a neighbor personally helped kill 182 bears over a 2-year period within a 16-kilometer radius of their property in the Big Thicket.

The culmination of the survey was the 1905 publication, *Biological Survey of Texas* (Fig. 3), which was authored by Bailey and included information about life zones, reptiles, and mammals (Bailey 1905). Oberholser made his study of the bird life of Texas a life-long project; his report did not appear until 1974 (Oberholser 1974).

The Archival Project

The 1905 and 1974 publications are only a small part of the information generated by the survey. Other archival materials included scientific specimens of birds, mammals, and reptiles, museum catalogs of the scientific specimens, field-trip diaries describing the travels of the field agents, detailed biological reports of significant events, physiographic reports of each place visited in Texas, special correspondence with landowners and field agents, and the photographs previously described. These archival materials represent a detailed depiction of Texas natural history at the turn of the century.

Bailey's 1905 book has been out of print for more than 75 years. The associated

Photo 3015, National Photographic Archive, Washington, D.C.

Fig. 1. Lacey's Ranch near Kerrville, Kerr County, Texas, 1906.

Photo 7236, National Photographic Archive, Washington, D.C.

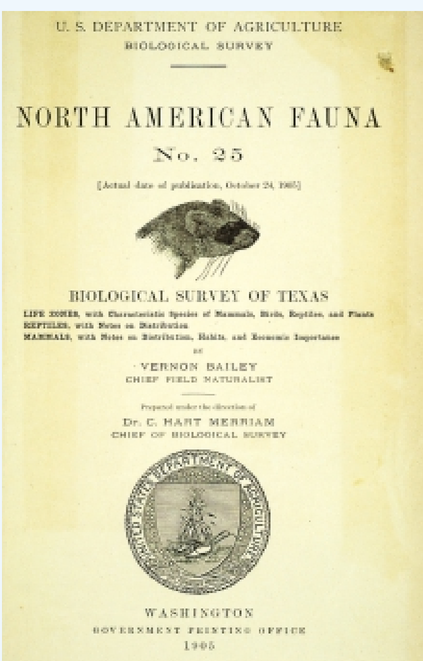
Fig. 2. Ab Carter, a bear hunter, stands next to a bear-gnawed tree near Tarkington Prairie, Hardin County, Texas, 1904.

archival materials are deposited at the Smithsonian Institution, but most modern biologists are unaware of the full scope of information that exists. In 1992 a project was initiated to document the archival natural history information from the Texas biological survey. The project has two objectives: to publish an annotated version of the original *Biological Survey of Texas* and to create a series of computer data bases by using the original documentation.

Five data bases of historical data are being created:

- Data base 1—a directory to the location of all files archived in the Smithsonian Institution;
- Data base 2—a description of each photograph available from the biological survey of Texas;
- Data base 3—the original survey reports (mammal, bird, plant, and physiography);
- Data base 4—field journals of the field agents; and
- Data base 5—specimen catalogs of the field agents.

The information obtained from current biological surveys of the state will be greatly enhanced by the availability of this historical data to document changes in species distribution, abundance, and diversity, as well as changes in land use. These historical documents also provide insight into public attitudes and the role of government agencies in conservation issues at the turn of the century.



U. S. DEPARTMENT OF AGRICULTURE
BIOLOGICAL SURVEY

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BIOLOGICAL SURVEY OF TEXAS

LIFE ZONES, with Characteristic Species of Mammals, Birds, Reptiles, and Plants
REPTILES, with Notes on Distribution
MAMMALS, with Notes on Distribution, Habits, and Economic Importance

BY
VERNON BAILEY
CHIEF FIELD NATURALIST

Prepared under the direction of
Dr. C. HART MERRIAM
CHIEF OF BIOLOGICAL SURVEY

WASHINGTON
GOVERNMENT PRINTING OFFICE
1905

Fig. 3. The title page of North American Fauna, *Biological Survey of Texas*, published in 1905 and authored by Vernon Bailey.

Changes in Texas Ecosystems

Mammals illustrate some of the patterns of faunal change in Texas during this century. Mammals and birds were the major types of vertebrates featured in the historical biological survey, and the publication of a recent book (Davis and Schmidly 1994) summarizing the current status of mammals provides a context for understanding change in this highly visible component of the fauna. The mammal survey by the federal biologists was comprehensive; Bailey documented 119 of the 141 native terrestrial species of mammals (about 85%) that occur in Texas today. The only group he failed to document accurately was bats (17 of 32 species), which is not surprising given that mist nets and modern bat-detection techniques were unavailable. Nine new taxa of mammals were described from material collected during the survey.

Although a detailed analysis of the archival material is not yet complete, some general statements can be made about past conditions and the extent of change in this century. For mammals, the most significant changes include the extinction of populations, subspecies, and species; introductions of nonindigenous species; and major changes in species or subspecies distributions.

Species extinctions have been common. By 1905 the only species of mammals extirpated from Texas were bison, grizzly bear, and elk, although several other species, such as beaver, black bear, spotted cats (ocelot and jaguar), pronghorn, and bighorn sheep, were markedly reduced in distribution or in numbers. Today, the gray wolf, red wolf, black-footed ferret, jaguar, margay, and the bighorn sheep have also been extirpated from the state.

Since the turn of the century, however, a few species have expanded their ranges—the nine-banded armadillo and the northern pygmy mouse are notable examples among mammals (Figs. 4 and 5)—whereas others, such as the pronghorn (Fig. 6), have undergone drastic range reductions. Entire populations of some subspecies, such as the hog-nosed skunk in the Big Thicket, have become extinct (Davis and Schmidly 1994).

Nonindigenous species, which were never encountered by Bailey, now openly range over much of the state. A prime example is the nutria, which was introduced into the state in the 1930's and now occurs

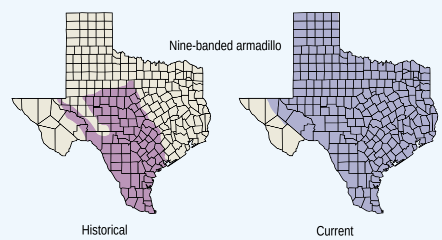

Fig. 4. Historical and current range of the nine-banded armadillo in Texas (adapted from Davis and Schmidly 1994).

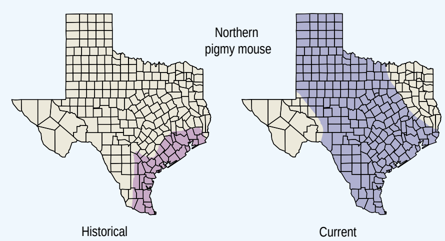

Fig. 5. Historical and current range of the northern pygmy mouse in Texas (adapted from Davis and Schmidly 1994).

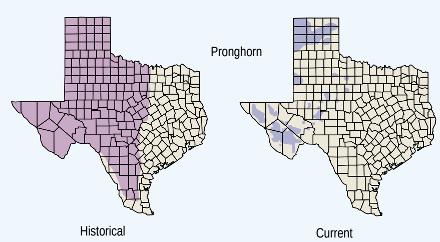

Fig. 6. Historical and current range of the pronghorn in Texas (adapted from Davis and Schmidly 1994).

over most of the eastern half of Texas and is still expanding its range. Ungulates introduced from Africa and Asia now occupy rangelands in proliferating numbers. During the 1990's, a colony of feral Japanese macaques even became established in south Texas.

Anthropogenic pressures on wild species today are totally different from those earlier in the century. In the early 1900's, overexploitation resulting from unregulated market hunting was a serious threat to wildlife. Poisoning, trapping, and unrestricted killing decimated many species (Fig. 7). Today, hunting of game species is an important management tool regulated by state law, and the revenue from hunting has become an effective market incentive for landowners to manage for wildlife habitat. Likewise, there are laws to prevent unregulated taking of endangered or threatened nongame species.

Today, the problems are mostly those related to wildlife habitats that have been destroyed, altered, and fragmented. Loss of critical habitat is the most serious threat to the modern fauna. Early Texas was a magnificent place, with a tremendous diversity of habitats, but human population growth and settlement through the past two centuries have significantly affected the state. Among the most altered places are prairies and grassland habitats, wetlands, riparian and riverine ecosystems, and the rangelands of the Edwards Plateau, Rolling Plains, the South Texas Plains, and the Texas Panhandle (Sansom 1996). When Texas entered the Union, it was the largest prairie state, but today fewer than 2,025 hectares of the original 5 million hectares of blackland prairies remain. Texas has lost more than 60% of its wetlands and about the same percentage of its bottomland hardwood forests (Baker 1995).

Comparison of old photographs taken by the survey field agents with modern landscapes from the same areas help document local habitat change. Bailey and his survey party were the first to survey wildlife in the Big Bend region of Texas, in what is today part of Big Bend National Park. One of their photographs (Fig. 8), taken at a working cattle ranch and farm near the mouth of Santa Elena Canyon, depicts open habitat and cottonwood trees along the river. Today this region is covered with a dense stand of river cane and introduced saltcedar, with few native cottonwoods. It becomes evident when assessing the old photographs that the amount of natural, unpolluted surface water has declined greatly this century. Almost every photograph those agents took of a stream or river showed abundant natural surface water (Figs. 9 and 10), which is not true of most of those places today, although the total amount of surface water in the state is probably greater today because of the construction of tens of thousands of tanks and large reservoirs.

A little-appreciated but important factor affecting natural ecosystems in Texas today has been the rapid change in the land-tenure systems (Sansom 1996). Unfortunately, an unprecedented breakup of family lands is now occurring in many places, brought about by changing economic conditions, inheritance taxes, and a state financial structure that is extremely dependent on property taxes. For example, throughout much of central Texas, where only tiny remnants of the native landscape survive today, the average tract size in many counties has dropped in this generation alone from thousands of hectares to fewer than one hundred. These areas, which once provided large blocks of land for wildlife habitat and outdoor recreation, now consist of tiny plots of introduced vegetation that cannot sustain the native wildlife. Meanwhile, the fear of litigation and regulation has closed off lands whose owners once welcomed and cooperated with scientists and conservationists.

Photo 26611, National Photographic Archive, Washington, D.C.

Fig. 7. Trapper catch for 20 February 1904 (coyotes, bobcats, ocelots, raccoons) from Sauz Ranch, Cameron County, Texas.

Photo 9048, National Photographic Archive, Washington, D.C.

Fig. 8. Lower entrance to Santa Elena Canyon of Rio Grande, Brewster County, Texas, 1901.

Conservation Challenges

Successful wildlife conservation in Texas requires finding a way to involve landowners in a positive way by providing them incentives to manage for wildlife habitat and to cooperate with scientists and state and federal land managers in conservation programs and practices (Bartlett 1995).

No effective conservation can exist without the support, participation, and cooperation of private landowners, many of whom fear that scientific knowledge will be used to usurp their landowner rights. Again, a valuable lesson can be learned from the old biological survey. The federal agents who worked in Texas relied on landowners for much of their information, and they saw the survey as benefiting landowners.

To conserve its wildlife diversity, Texas faces a daunting challenge. If conservation is to be successful, it is imperative that disparate groups (landowners, private conservation organizations, commodity groups, and state and federal agencies) begin to communicate, build trust, and find consensus solutions that satisfy the goals of society. To avoid past mistakes we must understand what has happened to our fauna and flora. Conservationists working in Texas are fortunate in having a baseline inventory that provides a detailed and scientifically accurate description of the entire state. This archival information base can be exceptionally useful as we develop and implement future management strategies for our wildlife resources.

Photo 6144, National Photographic Archive, Washington, D.C.

Fig. 9. First Creek, Lipscomb County, Texas, 1903.

Photo 3187, National Photographic Archive, Washington, D.C.

Fig. 10. Tierra Blanca Creek, near Hereford, Deaf Smith County, Texas, 1901.

Acknowledgments

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See end of chapter for references

Author

David J. Schmidly*
Department of Wildlife and Fisheries Sciences
Texas A&M University
College Station, Texas, 77553-1675

*Current address:
Department of Biological Sciences
Texas Tech University
Lubbock, Texas, 79409-1033

Environmental Change in South Texas

South Texas is bounded on one side by Mexico and the Rio Grande River and on the other side by the Gulf of Mexico and its barrier islands and bays (Fig. 1). Between these boundaries lies the Texas Lower Rio Grande valley, one of the nation's most important agricultural regions, producing fruit, vegetables, sugarcane, grain, cotton, and beef. Sensitive or imperiled environmental resources of south Texas include native Tamaulipan brushlands, the seagrasses and tidal flats of Laguna Madre, and the Rio Grande itself.

Fig. 1. South Texas.

The most important human-caused components of environmental change over the last 30 years have been water diversion and flood control, brushland clearing, human population increases, contaminants, and continued dredging of the Intracoastal Waterway in Laguna Madre. Extensive agriculture has fragmented and reduced the areas of native ecosystems. The North American Free Trade Agreement will play an as-yet unknown part in the future of environmental change in south Texas. In addition to human effects, parts of the Rio Grande watershed have been in a severe drought since 1993, exacerbating water quantity and quality problems. Also, an unprecedented chrysophyte algal bloom, known as the brown tide, has persisted in the Laguna Madre for more than 5 years.

Tamaulipan Brushland

Tamaulipan brushland is a unique ecosystem that dominates the Lower Rio Grande valley. Although Tamaulipan brushland is composed of several distinct biotic communities, all are characterized by dense, woody, and usually thorny vegetation and high biological diversity (Jahrsdoerfer and Leslie 1988). Vegetation is taller and lusher in the riparian areas (Fig. 2) than in the dry uplands (Fig. 3). Uplands are sometimes veined with thin riparian areas known as *ramaderos*, which not only provide important nesting and feeding habitat but also serve as corridors for animal movement. Tamaulipan brushland is home to more than 600 vertebrate species and more than 1,100 species of plants (Jahrsdoerfer and Leslie 1988). Many animals and plants of this area are found nowhere else in the United States, including two endangered cats, the jaguarundi and the ocelot.

Clearing of Tamaulipan brushland for agriculture started in the early 1900's. By 1988 more than 95% of all brushland habitat had been cleared for agricultural or urban use, including more than 90% of the riparian habitat (Fig. 4). Little of what remains in private holdings is expected to last until the end of this century. Remaining brushland often occurs in small, fragmented pieces, which are not in themselves capable of supporting the naturally high biological diversity of this ecosystem (Howe et al. 1986). To preserve and integrate what remains of this unique habitat, the U.S. Fish and Wildlife Service is purchasing land and easements in the Lower Rio Grande valley to form the Rio Grande Valley Wildlife Corridor, which now includes 25,000 hectares of federally managed land; the U.S. Fish and Wildlife Service plans eventually to double that amount (L. Ditto, U.S. Fish and Wildlife Service, McAllen, Texas, personal communication).

Fig. 2. Riparian area in Tamaulipan brushland, Santa Margarita Ranch.

Laguna Madre

Laguna Madre extends the whole length of the south Texas coast from Corpus Christi Bay to the Mexican border. It is 200 kilometers long, with a maximum width of

Fig. 3. Upland vegetation in Tamaulipan brushland, with palmettos.

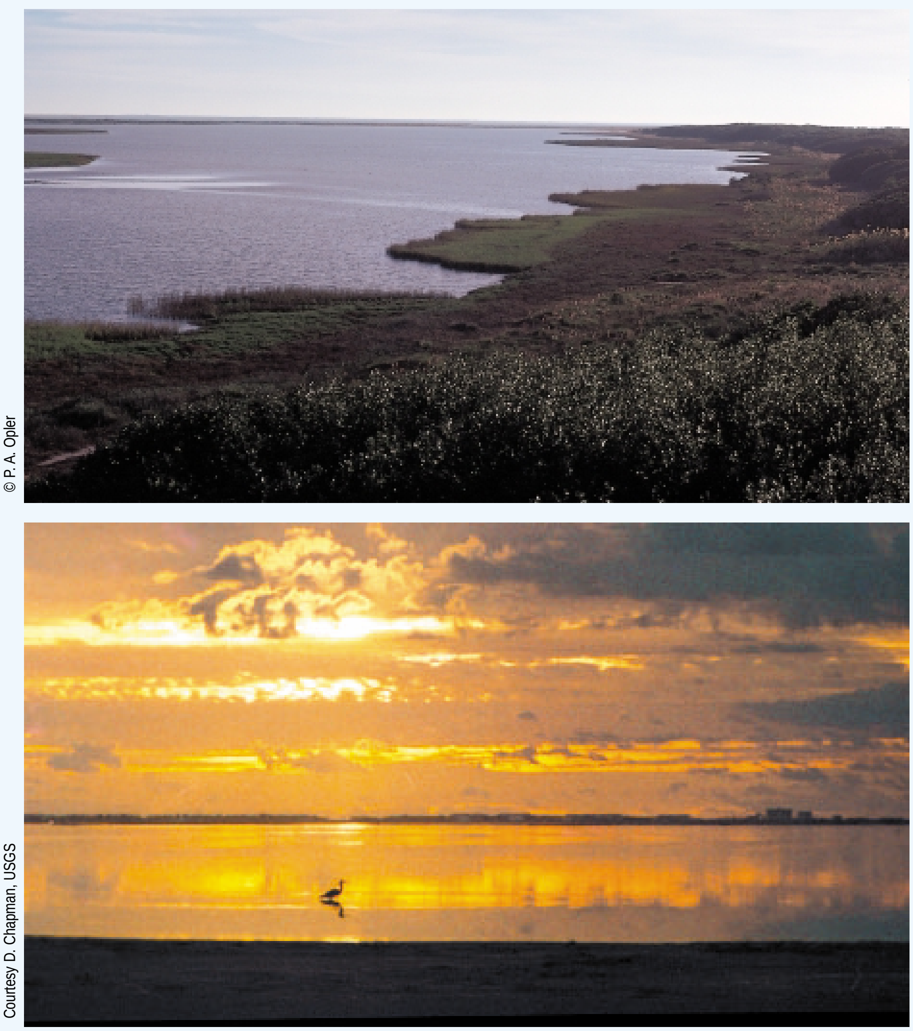
Courtesy A. Coykendall, U.S. Fish and Wildlife Service

Fig. 4. The clearing of Tamaulipan brushland.

11 kilometers, and is one of the few hypersaline lagoon systems in the world. Laguna Madre supports 75% of Texas's seagrass meadows (Fig. 5). The status of seagrasses in Laguna Madre is a great concern to resource managers because seagrass meadows are valuable nursery areas for wildlife. One species of seagrass, shoal grass, is the sole food of redheads on their most important wintering area. Between the mid-1960's and 1988, in the lower Laguna Madre, seagrass cover was lost over 150 square kilometers because of reduced water clarity caused by maintenance dredging (Onuf 1994). Seagrass was displaced over another 190 square kilometers as a result of long-term salinity moderation. The principal causes of salinity moderation were the excavation of a permanent water connection between the upper and lower Laguna Madre in 1949 (the Gulf Intracoastal Waterway) and the increased base flows from Arroyo Colorado and other agricultural drains (Quammen and Onuf 1993). Although seagrass cover increased in the upper Laguna Madre over the same period, the lagoon as a whole suffered a 30% decline of seagrass between the mid-1960's and 1988.

Since June 1990, brown tide, a monospecific algal bloom of unprecedented duration, has occurred in Laguna Madre. The brown tide is most concentrated in the upper Laguna Madre, except in winter when the focus shifts to the northern part of the lower Laguna Madre under the influence of the strong north winds accompanying cold fronts. Although high salinity and a nutrient pulse from a fish and invertebrate kill caused by a hard freeze promoted the development of the bloom, its unprecedented persistence is not understood (Stockwell et al. 1993). Contributing factors include low levels of zooplankton grazing on the brown tide alga, limited flushing of the lagoon, and the input of added nutrients, all of which require further investigation to determine whether management is feasible. Shading of seagrasses by the brown tide resulted in reduced seagrass biomass in deeper parts of upper Laguna Madre in 1991 compared with 1988 and even more severe reductions in 1992. By 1993, 3 square kilometers of seagrass meadow were bare, and by January 1995, the holes in the meadow had expanded to 9 square kilometers. Based on minimum light requirements of seagrass, 20–30 square kilometers will be bare by the time the distribution of zooplankton reaches a steady state with the brown tide-influenced light regime (Onuf 1996).

Plans are now in place for construction of the Gulf Intracoastal Waterway in Mexico. Expanded use of the canal system will increase the need for methods of dredge material disposal that will protect seagrass resources by minimizing effects on water



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Courtesy D. Chapman, USGS

Fig. 5. Laguna Madre and its fringing salt marshes.

clarity. Also, disposal of dredge materials may interrupt the necessary hydrological connection between the lagoon and the fringing expanses of wind tidal flats. Although these tidal flats are infrequently flooded, they support dense blue-green algal mats, are essential habitat for species of concern such as piping plovers, snowy plovers, and reddish egrets, and are important staging areas for peregrine falcons. Appropriate placement of dredge materials will be critical to the conservation of biological resources along the waterway as it is constructed through Mexico's Laguna Madre.

Irrigation, Water Diversions, and the Rio Grande

The Rio Grande is almost 3,200 kilometers long, the second-longest river in the United States. Despite this length, it is dwarfed in discharge volume by many of the nation's other rivers. Although the Rio Grande's snow-fed beginning is in the Rocky Mountains of southern Colorado, the river winds most of its length through hot and arid regions. Because of water withdrawals and drought, some stretches occasionally are completely dry. In these arid lands, the Rio Grande's water is critical to native flora and fauna and to human development. Between 243,000 and 283,500 hectares of land are irrigated each year by Rio Grande water in the Lower Rio Grande valley alone. This amount has remained fairly constant over the last 40 years because little additional appropriate uncultivated land remains (Fig. 6).

The Lower Rio Grande valley is not truly a valley but a broad delta with a single existing distributary, the Arroyo Colorado, which is now disconnected from the river. In the Lower Rio Grande valley, irrigation water that does not evaporate does not return to the river, as would be the case for most irrigated areas. Instead it passes through drainage systems into the Arroyo Colorado and the North Floodway, which function as huge drainage structures for the Lower Rio Grande valley. Municipal and industrial discharges are also added to the Arroyo Colorado, which eventually empties into the Laguna Madre approximately 72 kilometers north of the Rio Grande's mouth. Although the Arroyo Colorado is used for recreation, it is highly contaminated, and pollution-induced oxygen depletions are common (Jahrsdoerfer and Leslie 1988).

The hydrology of the Rio Grande is tightly controlled for much of its length by dams and channelization. Withdrawals for irrigation and municipal use occur along the length of the Rio Grande and its tributaries. Because of upstream diversions, most of the water that the Rio Grande delivers to the lower valley is attributable to the Rio Conchos, a tributary that drains the state of Chihuahua in Mexico (Vi Risser 1995). As is true in most desert regions, annual precipitation in Chihuahua is highly variable and results in corresponding variability in the Rio Conchos discharge (Fig. 7). The Chihuahua province was in a severe drought between 1993 and 1996. Discharge from the Rio Conchos in 1995 was extremely low, and the Rio Grande in the Big Bend National Park and the 314-kilometer section of the Rio Grande designated as a National

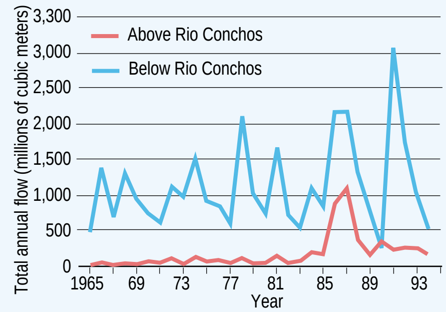

Fig. 7. Total annual flow of the Rio Grande at sites above and below the confluence of the Rio Conchos, in millions of cubic meters. Data from the International Boundary and Water Commission.

Wild and Scenic River were barely flowing during parts of 1995 (J. Cisneros, National Park Service, Big Bend National Park, personal communication).

As a hedge against future droughts, the Mexican government plans to increase water-holding capacity in the Rio Conchos watershed. In the long term, this will likely reduce the water that reaches the Rio Grande. Ironically, the Colorado and New Mexico mountains have experienced heavy snowfall in recent years, and New Mexico reservoirs are full. Because of legal water rights, little of this water is available to Texas and Mexico downstream of El Paso (Vi Risser 1995). Other rivers, such as the Pecos and Devil rivers on the United States side and the San Juan and Salado rivers on the Mexican side, join the Rio Grande below the National Wild and Scenic River section. Much of the water from these rivers is also diverted for agricultural and municipal use. Water diversions have reduced yearly average flow in the lower part of the Rio Grande by 30% to 50% (Edwards and Contreras-Balderas 1991). Despite and because of such reductions, Webb County has recently proposed that a new dam be built just above the city of Laredo.

Humans have altered the natural cycle of flooding in the Lower Rio Grande valley, which has decreased the quality and number of wetlands, especially the oxbow lakes known as *resacas*, an important wildlife habitat. Altered flood cycles in the Lower Rio Grande valley contribute to replacement of mesic riparian woodland trees with more xeric species such as mesquite (Jahrsdoerfer and Leslie 1988). Loss of the flood cycle has also been implicated in recent increases in nonindigenous species; native species are adapted to the periodic disruptions, which probably kept the nonindigenous species in check (Edwards and Contreras-Balderas 1991). The effects of channelization in the

Fig. 6. Low water flows in the Rio Grande below Falcon Dam.

Rio Grande have not been studied, but in general the negative effects of channelization on aquatic and riparian biodiversity are well known.

Agricultural Contaminants

Agricultural chemicals (insecticides, herbicides, and fertilizers) are used year-round in the Lower Rio Grande valley. In 1986 more than 100 different chemicals were used on crops throughout the region (U.S. Fish and Wildlife Service 1986). Six intensively used pesticides are atrazine, aldicarb, dicrotophos, methomyl, carbofuran, and dicamba (Bryant et al. 1993; see chapter on Environmental Contaminants). Agricultural chemicals reach surface waters through aerial application and subsequent drift and overspray, field runoff, and irrigation return flows. Resacas and other aquatic environments accumulate contaminants in their sediments. The Arroyo Colorado and other agricultural drains route potentially dangerous amounts of agricultural, municipal, and industrial contaminants to the Laguna Madre, a sensitive, shallow estuary that has little water exchange with the Gulf of Mexico (White et al. 1983; Custer and Mitchell 1987, 1991).

The proximity of agricultural lands to Lower Rio Grande valley refuges and the importance of the valley as a migratory bird flyway increase the potential for adverse effects on fish and wildlife. The aplomado falcon, an endangered species recently reintroduced at Laguna Atascosa National Wildlife Refuge, feeds on dragonflies, other insects, and small birds that may be accumulating contaminants from cultivated fields. A study of mosquitofishes from the Lower Rio Grande valley demonstrated that fishes can develop inheritable resistance to the lethal effects of pesticides (Andreasen 1985). Organisms that accumulate high concentrations of contaminants are a potential threat to species higher on the food chain.

Irrigation of salt-bearing soils in the region often results in return flows with a high dissolved salt content. Salinity in some agricultural drains regularly exceeds four parts per thousand (International Boundary and Water Commission 1992). The Pecos River is a major contributor to salinity of the Rio Grande because of natural salt deposits within the New Mexico portion of its watershed. Increased salinity in the Rio Grande negatively affects native fishes and encourages invasion by nonindigenous species such as the salt-tolerant blue tilapia, now the dominant fish species in the Brownsville area. Some reduced abundance of freshwater species also may be due in part to the expansion of salt-tolerant estuarine species upstream (Edwards and Contreras-Balderas 1991). Increased salinity threatens human use of the water as well, because water may become too salty for agricultural use and human consumption.

Industrial and Municipal Effects

Until 30 years ago, contamination in the Lower Rio Grande valley was primarily associated with agriculture. Since then, urbanization and economic development programs have significantly altered the border area. Today the valley is affected not only by chemicals and fertilizers from crop production but also by a wide range of municipal and industrial pollutants.

Maquiladoras are production plants in Mexico that process or assemble components from United States businesses into finished products, then send the products back to the United States. There are now 224 maquiladoras in the Mexican Lower Rio Grande valley, and until recently, the waste they generate has not been seriously regulated. Data pertaining to this waste are scarce, but it has been estimated that as little as 30% of maquiladora wastes are repatriated as required by United States–Mexico agreements, and that 98% of maquiladoras lack treatment systems for their wastewaters. Texas has recently developed a new tracking system for waste generated in Mexico, which may ameliorate part of this problem, but according to the World Bank, many maquiladoras are suspected of storing or illegally disposing of their waste by-products. The maquiladora industry was initially predicted to grow under the North American Free Trade Agreement by a moderate 7% to 10% per year, but these forecasts have been revised to 29% per year; the first 6 months of 1995 saw a 67% rise in maquila permits over 1994.

Mariculture, the cultivation of marine organisms, is a new and expanding agro-industry in the region and is an additional source of contaminants and nutrients to the Arroyo Colorado and the Laguna Madre. The threat of introduction of nonindigenous species and their diseases by mariculture operations is currently a high-visibility environmental concern.

Air quality in the Lower Rio Grande valley is affected by several sources, including localized problems due to vehicular traffic between the United States and Mexico, sugarcane burning, brick manufacturing, and maquiladora industries. A 1,400-megawatt, coal-fired electric generating plant across the border from Eagle Pass about 200 kilometers south of Big Bend National Park is of great concern. This plant, which recently became fully operational, is projected to contribute 250,000 tons of sulfur dioxide per year to the atmosphere.

Human population has sharply increased in the Lower Rio Grande valley over the last 30 years (Fig. 8), and because of poverty and the low tax base of the region, the infrastructure has not kept pace. Part of the population increase in the region is in impoverished, rural, unincorporated subdivisions known as *colonias*, which are characterized by substandard living conditions, most without sewage treatment systems. In 1995 there were approximately 1,400 colonias and 340,000 colonia residents in south Texas (Texas Water Development Board 1995). The number of people now living in colonias is about two-thirds of the entire 1970 population of the Texas Lower Rio Grande valley. Lack of sewage treatment in colonias contributes to contamination of groundwater and surface waters and is a human health problem. Release of untreated wastewater from Mexican municipalities into the Rio Grande is an even greater problem.

The Mexican population of about 8 million persons in the Rio Grande basin is 4 times the population on the United States portion of the Rio Grande watershed (Colorado, New Mexico, and Texas combined). Most of these people reside in cities with little or no sewage treatment (Texas Natural Resource Conservation Commission 1994). However, an environmental side agreement to the North American Free Trade Agreement created the Border Environment Cooperation Commission and the North American

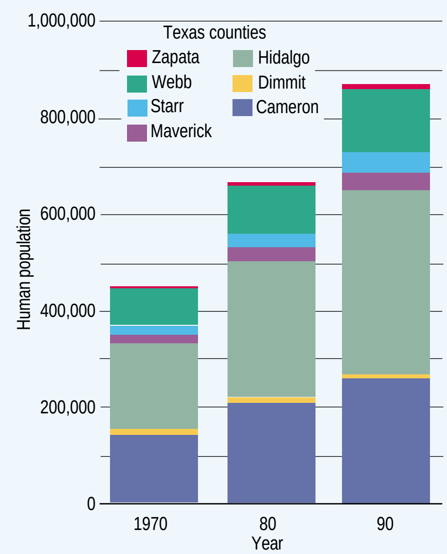

Fig. 8. Human population of Lower Rio Grande valley counties bordering the Rio Grande in Texas. Data from the U.S. Bureau of Reclamation (1995).

Development Bank, agencies charged with organizing and financing the environmental infrastructure of the region. Costs for wastewater treatment plants for Mexican border towns alone are expected to reach 2 billion dollars (Texas Natural Resources Conservation Commission 1994).

See end of chapter for references

Authors

Duane C. Chapman
Diana M. Papoulias
U.S. Geological Survey
Biological Resources Division
Environmental and Contaminants Research Center
4200 New Haven Road
Columbia, Missouri 65201-9634

Chris P. Onuf
U.S. Geological Survey
Biological Resources Division
Environmental and Contaminants Research Center
Texas Gulf Coast Field Station
Campus Box 339, TAMU-CC
6300 Ocean Drive
Corpus Christi, Texas 78412

the Appalachians, and more recently, gypsy moth infestations and dogwood anthracnose disease, both of which are increasing in the Southeast).

The old-growth stands represent only a part of the original productivity gradient. The most productive sites (moist, nutrient-rich sites on deep soils) were selected for and have generally remained in agricultural use. For example, the Great Valley (part of the Ridge and Valley province) between the southern Appalachians and the Cumberland Plateau in east Tennessee is dominated by farmland over large areas. Forests are restricted to dry sandstone ridges, most wetlands have been drained, and no old-growth forests remain.

Less than 0.1% of the original upland forests is estimated to have survived (Parker 1989; Martin et al. 1993b; Noss et al. 1995; White and White 1995). Stahle and Chaney (1994) reported a somewhat higher value (0.78%) for oak–hickory on poor, noncommercial sites in Arkansas. Davis (1995) described a total of only 237,061 hectares of known primary forest in the Southeast. In general, the surviving old-growth forests represent a biased sample of the original forests; they tend to be on steeper, drier, rockier, or wetter sites that were harder to farm or less valuable for harvest (reviewed by White and White 1995). These remnant stands have not received sufficient study for conclusions to be drawn about the differences in biological diversity that exist between old-growth and second-growth forests. Except for the mountains, remnants of old-growth forest are very small, mostly less than 100 hectares.

Even though most mountain forests were logged, Great Smoky Mountains National Park and several national forests protect exceptional remnants of old-growth forest, including some of the largest such tracts in the eastern United States. On mesic sites, trees reach 2.5 meters in diameter, 40 meters in height, and 300–500 years in age (Yost et al. 1994). In some unlogged forests, however, the nonindigenous chestnut blight fungus decimated one of the largest tree species, American chestnut, between 1920 and 1950 (Fig. 3). This species was widely distributed on environmental gradients, dominating submesic to subxeric sites, and was a consistent bearer of hard mast, an important resource for wildlife populations. Chestnuts grew in species-rich forests, and the species' competitors increased as it declined. No loss of vertebrate or plant species has yet occurred (chestnut sprouts continue to decline with age, indicating a gradual loss of the gene pool and species [Griffin 1992; Parker et al. 1993]), but at least one moth species has become extinct as the result of the chestnut decline (Opler 1978). In addition, several insects living in association with chestnuts were lost. Mesic old-growth forests dominated by other hardwoods and hemlock have been minimally affected by chestnut blight, but two other nonindigenous insect species now expanding toward the Southeast—hemlock woolly adelgid (found as far south as Virginia) and gypsy moth (detected in many

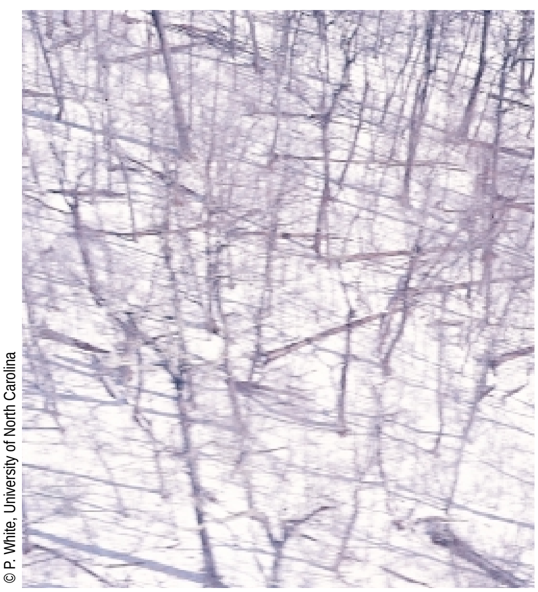

Fig. 3. Downed logs of American chestnut are conspicuous against a snowy background in the southern Appalachians. Eliminated as a dominant tree by the exotic chestnut blight from eastern Asia, the American chestnut was a forest dominant over wide areas of the eastern United States. Chestnuts were an important food for forest wildlife.

places in the Southeast but not yet causing outbreaks south of Virginia and the northeastern mountains of North Carolina)—have the potential of forever altering the last old-growth stands in the mountains just as another nonindigenous insect, the balsam woolly adelgid, has already drastically altered the high-elevation, old-growth spruce–fir forests saved from logging.

Duffy and Meier (1992) stimulated an important controversy in reporting that logged stands had lower diversities of spring wildflowers than old-growth stands (Elliott and Loftis 1993; Johnson et al. 1993). Meier et al. (1995) confirmed earlier results and argued that other taxa, such as salamanders, also show negative long-term effects of clear-cut logging. Although the trend has certainly been toward lower diversity for most groups, more work is needed on the effects of past land-use practices on biological diversity in the southern Appalachians and on techniques to restore previously farmed or logged lands to their former conditions.

Inventories are now under way on federal lands to map and evaluate the remnant old-growth stands (for example, Yost et al. 1994). These inventories will be critical for drafting a regional plan for the conservation of these unique remnants of the presettlement Southeast.


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Fig. 4. Creole pearly eye, a butterfly whose caterpillars feed on switch cane. This insect is limited to swamp forests and dense cove forests in the Southeast.

Fire Suppression

Fire was and is important to many southeastern ecosystems, including many Coastal Plain and south Florida ecosystems, pine-dominated forests of the Coastal Plain and Appalachian Highlands, oak and oak–hickory forests, oak savannas, glades, barrens, and prairies. Because most natural communities in the Southeast are dependent on fire, more than 50% of the rarest plants in the region also possess this dependence. Fire may also explain the occurrence of canebrakes, dense stands of the Southeast's only native bamboo, which were frequently described by earlier travelers but which have vanished from the landscape except for small remnant patches (Noss et al. 1995; Fig. 4). Although natural fires were quite important, Native Americans and European settlers also set fires frequently. When fire suppression became effective in the 1940's, dramatic changes in ecosystem composition and structure began.

Pine dominance was produced by intense fires, with subsequent lower intensity fires reducing competing hardwoods in the pine understories. Given the age of pine stands, intense, stand-initiating fires must have occurred at least once every 100–200 years; less intense fires occurred much more frequently—every 2–12 years. In the absence of fire, oak, hickory, and pine replace longleaf pine on the Coastal Plain (Stout and Marion 1993), and oak-dominated forests replace pitch pine and Table Mountain pine on the dry ridges of the Appalachians. The net trend of these landscapes is away from pine-dominated ecosystems, leading to declines in species associated with those systems.

Outbreaks of the native southern pine beetle can not only hasten the succession from pine to hardwoods but can also result in high fuel loads. On dry topographic sites and in drought years, high-intensity fires can occur because of these fuel loads. Such hot summer fires are critical to pine regeneration.

Although oaks and hickories increase on the driest sites with reductions in fire, these trees are declining on moister sites where fire was important in limiting mesic hardwoods (Christensen 1977). Thus, throughout the Southeast, there is a general trend toward an expansion of mesic species and a contraction of dry-adapted and fire-dependent species. Understory stem densities have also increased. A failure of oak to regenerate on sites where the species now dominates is a widely observed phenomenon in the eastern United States. McGee (1986) and other researchers hypothesized that this change is caused not only by fire suppression but also by other factors such as air pollution (Kessler 1989). Low fire frequencies have also allowed woody plants to invade the glades, barrens, and prairies once associated with oak and hickory forests. Early descriptions of the southeastern landscape suggest frequent forest openings, larger areas of grassland and savanna, and upland forests with open understories (Skeen et al. 1993).

Changes in Hydrology and Water Quality

Alteration to the hydrological regime is a common disturbance in a variety of southeastern ecosystems: bottomland and floodplain forests, mountain bogs, rocky stream gorges, longleaf pine savanna, Carolina bays, pocosins, Atlantic white-cedar swamps, barrier-island communities, mangrove forests, rivers, streams, caves, lakes, and the Everglades mosaic of communities. Hydrological change has altered flood depth, duration, frequency, and seasonal timing in many of these systems, leading to a raising and lowering of the water table in specific cases.

Hydrological change is caused by sedimentation, construction of dams and other barriers, and channelization (Adams and Hackney 1992). Portions of almost all major southeastern rivers have been impounded during the last 75 years. For example, a 1974 stream survey in Maryland showed that all 14 drainages in 17 tidewater counties had dams (258) or other blockages (89; Lee et al. 1984). Other barriers include farm or mill pond dams, weirs, and raised culverts. Dams result in changes to water temperature and unpredictable releases of water. Channelization, which includes straightening the streambed, smoothing bottom contours, and removing logs, obstructions, and plants, alters the rate and timing of water flow (the local water table is lowered, resulting in increased flooding downstream), aquatic productivity, microhabitats within the channel, and food webs. Sedimentation, blockages, and channelization often occur within one river system, leading to decreases in native fishes and other aquatic species, a loss of species intolerant of such changes, and increases in tolerant species and nonindigenous species (Crumby et al. 1990).

The dynamics of flooding and meandering rivers are a major natural process in southeastern ecosystems. Many plant and animal species are dependent on the natural dynamics of water flow. The overall tendency is for human influence to make a dynamic environmental factor less variable. Succession favors the species best adapted to the more uniform conditions, and diversity decreases. In natural systems, however, extreme hydrological events are an important agent in the maintenance of species diversity.

Other factors responsible for depletion of aquatic faunas are pollution (including chemical and thermal pollution) and introduction of nonindigenous fishes and aquatic plants. Invasive nonindigenous plants that are capable of altering function (for example, hydrology, amount of photosynthesis, and food webs) in aquatic systems in the Southeast include Eurasian watermilfoil, hydrilla, parrot feather watermilfoil, curlyleaf pondweed, water hyacinth, and water chestnut (Hotchkiss 1967; Lachner et al. 1970).

In recent years, the Clean Water Act has done much to reduce point sources of pollution by requiring water treatment. Nonpoint-source pollution and sedimentation are harder to control, though. Sedimentation is a serious problem for most aquatic organisms, particularly primary producers as well as benthic (bottom-dwelling) macroinvertebrates and fishes that require gravel or rock substrates. Medium-sized rivers are particularly vulnerable to alteration of substrate composition and texture (Etnier and Starnes 1991).

Status and Trends of Southeastern Ecosystems

In this section, we review trends for ecosystems that are known or suspected to be experiencing loss of diversity. Our list was developed from Boyce and Martin (1993), Grossman et al. (1994), and Noss et al. (1995; Table 8). Because vertebrates often range across ecosystem types and reveal the linkage between terrestrial and aquatic systems, they often experience similar trends or threats across ecosystem types; for these reasons, we have included summary sections for fishes (in the aquatic section) and for reptiles and amphibians, birds, and mammals (at the end of the sections on ecosystems). In the course of this overview, we also present summary sections for other groups.

Table 8. Ecosystems discussed in this chapter, with cross-references to Boyce and Martin (1993), Grossman et al. (1994), and Noss et al. (1995). Boyce and Martin (1993) placed ecosystems of concern in three categories: resilient (upland areas that were still forested, though much affected by human impacts), threatened, and remnant or island-like (isolated habitats that were formerly more widespread than at the present, whether in historical or geological time).

Ecosystem	Boyce and Martin (1993)	Grossman et al. (1994)	Noss et al. (1995)
Widely distributed			
Upland forest	Resilient	x	x
Bottomland forest	Threatened		x
Glade, barren, and prairie	Remnant	x	x
Mountains			
Spruce–fir forest	Remnant	x	x
High-elevation deciduous forest	Remnant	x	
Heath bald	Remnant		
Pine forests			
Mountain bog	Threatened	x	x
Grassy bald		x	
High-elevation cliff	Remnant	x	
Rocky stream gorge	Remnant	x	
Coastal Plain			
Longleaf pine forest	Remnant	x	x
Carolina bay	Threatened		x
Pocosin	Threatened		x
Atlantic white-cedar forest	Threatened		x
Maritime communities	Remnant	x	x
South Florida			
Tropical hardwood		x	
Slash pine		x	x
Florida sand pine scrub	Remnant		
Mangrove	Threatened		
Everglades	Threatened		

Southern Appalachian Mountains

Spruce–Fir Forests

The southern Appalachian spruce–fir forest is disjunct from and compositionally different from the spruce–fir forests of the central and northern Appalachians (White and Cogbill 1992). For example, 12 species of vascular plants, including the narrowly restricted endemic Fraser fir, a dominant tree, occur only in southern Appalachian spruce–fir forests. Although more than one-half of the original extent of spruce–fir forest was protected as old-growth forest in the 1920's and 1930's, two human-caused changes have forever altered these ecosystems: invasion by nonindigenous insects and air pollution.

Until large-scale logging began in the late 1800's, these mountain forests were undisturbed because they were too steep and remote for settlement by either Native Americans or Europeans (Pyle and Schafale 1988). The original extent of the southern Appalachian spruce–fir forest has been estimated as 12,100–14,200 hectares (White and Cogbill 1992), but by 1930 logging had reduced this total by about one-half (Saunders 1979). Slash fires and severe soil erosion often followed logging, and some damaged sites remain in herbaceous or shrub-dominated vegetation, even after at least 70 years of succession.

Conservationists, though, were successful in bringing 93% of the remaining spruce–fir forest into public ownership, including the East's largest block of old-growth, spruce–fir forest, which was protected when the Great Smoky Mountains National Park was established in 1934. At that time, 50% of the original old-growth spruce–fir forest seemed to have been securely protected, by far the largest fraction of any southeastern ecosystem. These forests, though, were to be forever altered by human influences that are less obvious than logging.

Red spruce, the most valuable tree of these forests, failed to regenerate on logged lands. In the 1930's, foresters began trials of a variety of conifers in an early attempt at restoration. Unfortunately, these trials were probably the means by which a Eurasian insect, the balsam woolly adelgid, entered the southern Appalachians (Fig. 5). This pest proved devastating for the narrowly restricted endemic Fraser fir, a dominant of this system, and heavy mortality of this species began in the late 1950's. The pest has now spread throughout the southern Appalachians.

There is no practical way to eliminate the adelgid. Individual stands of Fraser fir (including fir plantations—Fraser fir is the South's most valuable and popular Christmas tree) and other trees can be sprayed, but this is costly and not always effective because of the difficulty of reaching all feeding sites on the trees. In the short term, seed samples of the genetic diversity of Fraser fir must be stored for possible future restoration.

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Fig. 5. The summit of Mt. LeConte, Great Smoky Mountains National Park, Tennessee, shows patches of green young trees that have not yet reached the stage in which they are vulnerable to balsam woolly adelgid, a nonindigenous insect from Eurasia. This insect has caused heavy mortality of the mature trees of a southern Appalachian endemic tree, Fraser fir. Acid rain possibly played a minor role in this mortality, but pollution has caused more dramatic effects in high-elevation streams and may be responsible for growth declines in red spruce, a codominant with Fraser fir in these mountain forests.

Because Fraser fir was a dominant tree of these forests, its sudden loss has resulted in high light levels and reduced soil moisture. Shrub biomass increases in the short term and may cause decreased population sizes of herbaceous understory plants, including rare disjuncts and endemics (Fig. 6). Lichens, mosses, and other species that occur specifically on the bark of Fraser fir may also be at risk. A newly listed species in this ecosystem is the spruce–fir moss

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Fig. 6. Moisture and shade-loving understory species of the southern Appalachian spruce–fir forest are drastically affected by the death of Fraser fir, including the rare northern beech fern, shown here in an undisturbed forest.

spider, a narrowly restricted endemic that has disappeared from several locations affected by the balsam woolly adelgid (K. Langdon, National Park Service, Gatlinburg, Tennessee, personal communication). Changes in populations of other species are probably also occurring. For example, Alsop and Laughlin (1991) showed that decline in the fir population caused a 35% decrease in the density of breeding bird populations, the loss of two forest interior bird species, and the gain of three bird species characteristic of successional vegetation.

The mortality of Fraser fir is an acute problem caused by a nonindigenous insect, whereas air pollution is producing changes that are less dramatic but potentially just as severe (Eagar and Adams 1992). The deposition of pollutants, which is altering soil and stream chemistry (Mulholland and Lenat 1992), increases with elevation and thus has been of particular concern within these high-elevation forests. Biotic effects in streams are being investigated (Mulholland and Lenat 1992).

In the 1970's, red spruce experienced heavy mortality in the Northeast (Eagar and Adams 1992). Mortality in southern Appalachian spruce–fir forests was never high enough to be attributed to pollutant exposure, but growth declines, although not universal, were widely reported (Eagar and Adams 1992). Even though multiple explanations for growth declines are being explored, a leading theory is that pollution causes an increase in the cycling rate for calcium and other cations, and that the increased mobility of calcium will result in its loss to streams (Johnson et al. 1992). This theory predicts a long-term decline in soil fertility in high-elevation forests.

When the first concerns about air pollution effects arose in the late 1970's and early 1980's, there were few baseline data for evaluating change in the spruce–fir ecosystem. We did not know the expected rates of growth or mortality, nor the dynamics of stand composition and structure. Neither did we have an understanding of soil chemistry or its relation to atmospheric deposition or the chemistry of stream waters that drained this system. The decade of research that occurred in southern Appalachian spruce–fir forests (1982–1992) under the National Acid Precipitation Assessment Program (some research continues on individual sites through other sources of funding) has produced a key data set to help evaluate future changes. This program involved remote-sensing imagery on several scales, surveys of pathological fungi and other organisms, permanent vegetation plots, soil analysis, analysis of ecosystem processes, intensive studies of the mechanisms of pollutant exposure, and surveys of terrestrial and aquatic animal populations. The results of this intensive study will aid future assessments of the status and trends of the spruce–fir ecosystem.

Pine Forests

Fire frequency in pine stands on dry topographic positions has decreased during the last 60 years from one fire in 8 to 12 years to one fire in thousands of years (Harmon 1982). Concomitant with this decrease in fire has been the succession from pine to hardwood dominance (Harmon et al. 1983). Four pine species dominated dry sites in the mountains: Virginia pine and short-leaf pine on low-elevation sites, pitch pine on low- to mid-elevation sites, and Table Mountain pine on mid- to high-elevation sites. Table Mountain pine is restricted to the Appalachian Highlands from Pennsylvania to Georgia and Alabama; it has persistent serotinous cones that release seeds only after intense fires (Williams and Johnson 1992; Fig. 7).

After intense fires, these pines become established over several years to a decade, resulting in stands with similar sizes and ages of trees. As these pines age, large patches become vulnerable to outbreaks of a native insect, the southern pine beetle. Although these beetles are a natural part of the system, pine beetle infestations can be alarming and are treated as loss of value in managed forests.

As the pines senesce, they are replaced by hardwoods, among which oaks are usually prominent. As the hardwoods themselves age

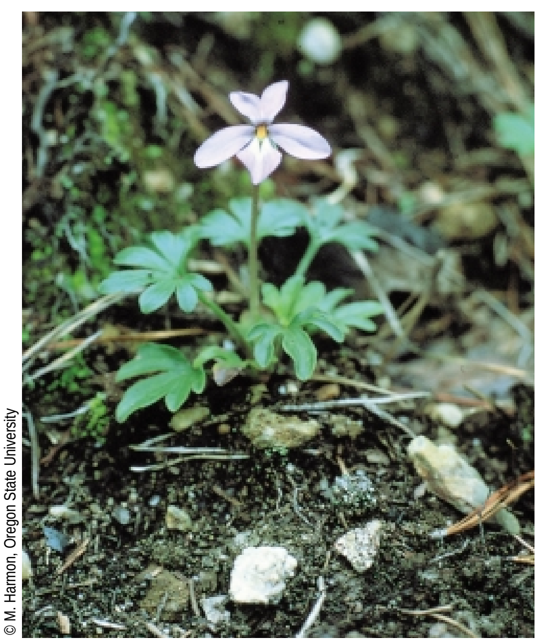

Fig. 7. Fire is an important natural process on dry slope positions in the southern Appalachian Mountains. Bird-foot violet flowers and fruits heavily after burning on Polecat Ridge in the Great Smoky Mountains. On such sites, pine regeneration, including that of the endemic Table Mountain pine, occurs only after fire.

and grow bigger, they become less vulnerable to fire because of their thicker bark (Harmon 1984). Concurrently, debris produced by the death of overstory pine is reduced by decomposition. Thus, over successional time, fire behavior becomes altered—fires will be less intense and will no longer produce pine regeneration.

Although we know that the southern Appalachians are experiencing a trend from pine to oak dominance on dry ridges (Harmon 1984), the rate of loss of pine ecosystems is the subject of ongoing research. We do not have a quantitative estimate of the number and rate of loss of fire-dependent species, although long-term research on these questions has begun.

Mountain Bogs

Mountain bogs, including true bogs and fens, are small (0.5–10 hectares), isolated wetlands (Richardson and Gibbons 1993). Compared with other mountain wetlands, such as alluvial and levee forests and floodplain pools, they contain high numbers of rare species (Earley 1989; Stewart and Nilsen 1993). These mountain wetlands are much less common in the unglaciated Southeast than in the glaciated north.

Human activity has greatly reduced the number and extent of mountain wetlands. Of the estimated 2,000 hectares of mountain wetlands that historically existed in North Carolina, only about 200 hectares remain. Most remaining mountain wetlands have been affected by timbering, development, and alterations to drainage (Smith 1994). The exact number of remaining bogs is difficult to determine but is most certainly fewer than 150 in the entire Southeast. Few of these are pristine, and most are very small (less than 1 hectare). More than half of the existing bogs are in private ownership and are under serious conversion pressure by private developers. About one-fourth of the remaining bogs are on federal property and are therefore protected, as are those few that are owned or managed by The Nature Conservancy (Richardson and Gibbons 1993).

Bogs have been destroyed by draining, grazing, mining, logging, off-road vehicles, agriculture, and development (Richardson and Gibbons 1993). They are further threatened by water-quality changes—silt loads from surrounding soil erosion and altered chemistry from agriculture (Smith 1994). Alterations to regional hydrological balances (excessive well drilling and pumping, for example) can also destroy bogs (Richardson and Gibbons 1993).

The bog turtle is a threatened species that inhabits mountain bogs and is protected by state laws in only part of its range. The turtle is frequently collected illegally for the pet trade, and collectors have exploited the differential protection status by claiming that they collect bog turtles from states where the species is unprotected. Rare orchids and carnivorous plants often suffer similar fates (Earley 1989). Once a bog has been discovered by a collector, that site is often revisited until all species of commercial value have been removed. As bogs are widely separated from each other, the opportunity for plants and animals to recolonize is minimal, and the site remains permanently diminished.

To date there are almost no quantitative vegetation studies of the Southeast's mountain bogs and fens (Richardson and Gibbons 1993). Intermittent fire and beaver activities are speculated to play a role in the origin and maintenance of these communities (Richardson and Gibbons 1993).

Grassy and Heath Balds

Though the southern Appalachians do not reach a high-enough elevation for a true climatic treeline (Cogbill and White 1991), two kinds of high-elevation treeless habitats occur—heath balds and grassy balds (Fig. 8). Heath balds are stable, low-diversity communities dominated by evergreen broad-leaved shrubs. In contrast, grassy balds are diverse open communities that are unstable and were originally dominated by herbaceous plants (Saunders 1980). Grassy balds do not have distinctive animal communities (however, Otte [1995] suggested that there are undescribed insect species in these habitats) but do support rare plant species, including northern disjuncts and local endemics (Stratton and White 1982).

Although a few grassy balds seem to predate the earliest influence of European settlement, many were created as summer pastures for livestock (Lindsay and Bratton 1979). All the balds have a history of livestock grazing, and when the animals were removed from the 1920's to the 1940's, trees and shrubs began to invade the grassy balds. No known natural processes create or maintain grassy balds—they do not form

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Fig. 8. Mountain laurel is a dominate of heath balds, invades grassy balds during succession, and is a frequent understory shrub in dry forests of the southern Appalachian Mountains.

on distinctive topographies or soils (Stratton and White 1982), and they occupy an extremely small percentage of the sites that are seemingly appropriate for grassy balds, as defined by the extant balds. A few balds may have been created by Native Americans during warmer climates of the past and then were maintained by human-set fires and the native grazing animals that are now extirpated (woodland bison and elk).

The southern Appalachian landscape had 73 grassy balds in the early 1900's (Pittillo 1980; Saunders 1980); the number has been reduced by succession to woody plants, and the size of balds has been reduced by 50% or more of the original surface area. At present, only a few balds are being managed for the open habitat. For example, of 30 original grassy balds in Great Smoky Mountains National Park, only 2 are being managed for the open condition. Although the future will probably bring further reductions in the number of grassy balds in the southern Appalachians, several that are important to rare plant populations are in federal ownership and are being managed for the open condition (R. Sutter and P. White, University of North Carolina, Chapel Hill, unpublished manuscript).

Cliffs and Rocky Stream Gorges

High-elevation rock outcrops support 45 rare plants, including northern disjuncts and southern Appalachian endemics (Wiser 1994). Wiser surveyed these communities at 44 sites, of which 7 were unprotected. Historical population losses are exemplified by mountain avens, a herbaceous perennial species that declined from 16 to 11 populations (Endangered Species Technical Bulletin 1990; Fig. 9). Cliffs are popular hiking destinations and are used by rock climbers. Recreational effects are significant in many areas (Wiser and White 1997), but data sufficient to establish regional trends on mountain avens and other species are not available.

The rocky stream gorges that drain the high mountains also support a number of narrowly restricted endemics, which exist in a tension zone between stream scouring and succession to upland forest. Artificial impoundments eliminate some populations through flooding and result in diminished flood scour for other sites, leading to an increase in plant competition that will reduce the other populations. These sites are also prone to adverse effects because of human recreational activities. One of the plants of these habitats is the narrowly restricted endemic Ruth's golden aster, known from only two rivers in east Tennessee. A multiagency project to monitor and protect this species was begun in 1986; researchers found that the species had declined by some 25%–33% from 1986 to 1995 at two of three populations on one river but appeared to be stable at the third site and on the second river (T. Smith and L. Collins, Tennessee Valley Authority, Norris, Tennessee, unpublished data). Regional data for other endemics or for this habitat in general are not available.

Fig. 9. The high-elevation endemic mountain avens is found on rock outcrops that harbor some of the South's rarest plants. Scientists are researching the air pollution sensitivity of these rare species in the Great Smoky Mountains National Park.

Ecosystems Found in the Piedmont and Coastal Plain

Bottomland and Floodplain Forest

The Southeast contains 36% of all wetlands and 65% of the forested wetlands of the conterminous United States, even though it makes up only 16% of this area (Keeland et al. 1995). Noss et al. (1995) estimated that 78% of southeastern wetlands were lost between settlement and 1980.

The forested wetlands of the Coastal Plain and Piedmont and the continental interior include bottomland hardwood forests and deepwater alluvial swamps (Sharitz and Mitsch 1993); 12 major forest types have been recognized. The vegetation of these forests varies in composition and structure according to flooding duration (Larson et al. 1981).

Harris (1989) listed characteristics of these ecosystems that are beneficial to wildlife: hard mast production and a phenology (that is, periodic biological phenomena, such as flowering and breeding, in relation to climate) that is not synchronous with surrounding upland communities, frequent cavity trees, high abundance and biomass of invertebrate wildlife, and a linear distribution throughout the landscape that aids local and regional movement of animals. The seasonal flooding of these habitats makes them less suitable for agriculture; thus, in agricultural landscapes, they are often the only forest refuges available for many mammals, birds, and other species. Bottomland forests were and are very important to many birds in the Southeast, and the extinction of one species, the Carolina parakeet, and the extirpation of another, the ivory-billed woodpecker, are partially the result of fragmentation of this habitat.

Southern floodplain forests may have the largest remaining area of any riparian habitat in the United States (Klopatek et al. 1979; Keeland et al. 1995). Estimates of extent vary widely, however, from 6,600,000 hectares (Klopatek et al. 1979) to 13,000,000 hectares (Abernethy and Turner 1987). This areal extent is decreasing (0.51% per year from 1954 to 1974; Harris and Gosselink 1990), with a total loss of about 63% (Klopatek et al. 1979) to 78% (Noss et al. 1995). These forests have been converted to farmland, industrial parks, and urban areas. Surviving stands are influenced by levee construction, channelization, agricultural runoff, cattle grazing, timber extraction, and invasions of nonindigenous species. Restoration has been attempted, with 65,000 hectares of bottomland forest replanted since 1985, but it is too early to tell if these efforts will be successful (Keeland et al. 1995).

Species and population losses accompany these trends in habitat loss. For example, in Louisiana, Burdick et al. (1989) showed that the number of forest bird species was 15% lower and the number of individual birds 33% lower on transects with 26% forest cover compared with those areas that had 46% forest cover.

Glades, Barrens, and Prairies

Scattered throughout the Southeast are naturally treeless areas that support plants and animals not found in surrounding forests (Fig. 10). These openings have been variously referred to as prairies, glades, and barrens. Historical accounts suggest that at the time of settlement these open habitats were more widespread and adjoined forests with more open understories than the forests of today (Delcourt et. al. 1986; Wilkins et. al. 1991; DeSelm and Murdock 1993; Martin and Boyce 1993). Such open habitats are now rare, occupying only a fraction of 1% of the Southeast’s natural landscape because of conversion to agriculture, quarrying,

Fig. 10. Purple coneflower is a species of open glades within closed deciduous forest. These habitats were maintained by frequent fire.

reduced fire frequency, and the loss of two large native grazers, the woodland bison and eastern elk. The naturally treeless areas that remain range in size from 0.25 hectares to as large as 17 hectares and are scattered over the region.

Upland open habitats occur in two settings. First, they are found on the thin soils of bedrock outcrops (hence, they are often treated as rock outcrop communities [Quarterman et al. 1993]). The bedrock itself may have unusual chemistry (the serpentine barrens) or interior drainage (the dry soils over some limestones). These rockier glades had little agricultural value but were used as rough pasture and for homesites, quarries, and dumping areas. The variation in rock types (limestone, diabase, granite, sandstone, shale, and serpentine), topography, climate, and disturbance history produces an array of communities; The Nature Conservancy’s national classification includes 40–50 different nonforested, open, herb-dominated communities (The Nature Conservancy and Environmental Systems Research Institute 1994). The most widespread community type is glades over limestone; this community type has been studied since the work of Quarterman in the 1950’s (Quarterman et. al. 1993). Twenty-nine endemic plants inhabit this community type, which is one of the highest numbers of endemic plants occurring in any southeastern habitat (Baskin and Baskin 1986, 1989; Sutter et al. 1994). The calcareous glades of Alabama and Tennessee support 21 plant species that are known globally from 20 or fewer locations (R. Sutter, The Nature Conservancy, Chapel Hill, North Carolina, unpublished data). Over half the glade sites have been destroyed, however, with fewer than 30 pristine or only slightly disturbed sites remaining. In Tennessee, 90% of ecologically intact limestone glades and 50% of the total glades area have been lost.

In the glades over limestone, the absence of a canopy allows the ground to be exposed to high temperatures and high amounts of sunlight; thus, the thin soils of some glades often have little water-holding capacity, producing a highly xeric (dry) habitat. In contrast, some glades experience waterlogging and pooling of water in late winter and early spring; these include the limestone cedar glades of Tennessee, Missouri, and Arkansas. These conditions are favorable for some species of winter annuals, such as the six species and four varieties of gladecress that are endemic to southeastern limestone glades (Baskin and Baskin 1986, 1989).

Larger grasslands (prairies and barrens) maintained by fire and grazing are the second kind of open habitat (DeSelm and Murdock 1993); only remnants of this vegetation exist. These larger grasslands (the Big Barrens of Kentucky and the Black Belt of Alabama and Mississippi) had deeper soils and were almost all converted to agriculture.

Although the overall rate of loss is unknown, three areas in Ohio and Tennessee experienced a reduction of this type of open habitat from 1.3% to 3.4% per year for 33 years (DeSelm and Murdock 1993). Prairies occurred in Kentucky (the Big Barrens: greater than 99% loss; Bluegrass Prairie: 100% loss [data from Noss et al. 1995]), Arkansas (the Grand Prairie: greater than 99% loss), Alabama and Mississippi (the Black Belt: greater than 99% loss), Mississippi (the Jackson Prairie: greater than 99% loss), Louisiana and eastern Texas (Coastal Prairie: greater than 99% loss), and Florida (St. John's River Prairie, Kissimmee River Prairie, and prairies west of Lake Okeechobee and in south Florida: virtually all converted to agriculture). Smaller grassland fragments occur throughout the region (DeSelm and Murdock 1993).

Animal species that have been extirpated from prairies and barrens include the greater prairie-chicken, which was extirpated by the early twentieth century from Kentucky grasslands; bison, which was extirpated from North Carolina by 1765, from Maryland by 1775, from Virginia by 1797, and last observed in the Southeast in 1825 (Webster et al. 1985); and eastern elk (Echternacht and Harris 1993). Today, southeastern grasslands are so small and so distant from extensive grasslands to the west that other grassland vertebrate animals do not occur in them, nor do they support locally endemic vertebrates (DeSelm and Murdock 1993). Many eastern animals, though, including rare bird species (Kale 1978; Hamel et al. 1982) and reptiles (Jordan 1986), use these open habitats, and studies of limestone and granite outcrops revealed endemic arthropod species as well (Quarterman et al. 1993). King (1985), for example, found several arthropod species endemic to the exposed rock areas of granite outcrops.

Some of the plant species of open habitats have persisted along roads and under power lines. For example, Schweinitz's sunflower has declined from 21 to 13 populations, all of which are on roads and under power lines (Endangered Species Technical Bulletin 1991). If appropriately managed, these populations can possibly be used to lessen the extinction risk in these species. Populations of smooth coneflower in a power line right-of-way in Granville County, North Carolina, mown at a 1- to 3-year interval by Carolina Power and Light, have thrived (Barnett-Lawrence 1994). Roadside populations, though, are vulnerable to roadway expansion and maintenance activities (Barnett-Lawrence 1994).

The Coastal Plain

Longleaf Pine and Southeastern Pinelands

The pinelands of the Coastal Plain once extended from the James River in southeastern Virginia to the Trinity River in eastern Texas and covered 24 to 35 million hectares (Frost et al. 1986; Stout and Marion 1993). Longleaf pine savanna was the most common community—the trees, which were thinly distributed, flat-topped, and had limbless lower trunks, occurred in a sea of grasses and diverse wildflowers and carnivorous plants. The historical distribution of pineland communities was determined by moisture supply and fire (Frost et al. 1986). Pines were dominant in habitats ranging from pine flatwoods and mesic savannas to the longleaf pine–turkey oak association in the dry Carolina Sandhills. Longleaf pine was the leading species, with slash pine increasing southward. Both species are now outnumbered by loblolly pine because of fire suppression, conversion to farmland, and commercial timber production (Ware et al. 1993).

The most widespread of the pineland communities, the longleaf pine savanna, occurred widely on the moisture gradient from wet areas and mesic savannas to the dry sandhills and turkey oak associations (Fig. 11). The vast, parklike longleaf pine savanna had an herbaceous layer dominated by wire-grass in the southeastern states (Fig. 12) and by bluestems in Louisiana and eastern Texas. At small scales (1–100 square meters), this herb layer is one of the most diverse in the world (40–75 species of vascular plants have been reported for a single 1-square-meter quadrat and 130 for a 0.1-hectare plot [Clewell 1989]). Today, only 14% of the expansive longleaf pine forest remains,

Fig. 11. Dry sandhill scrub, Emanuel County, Georgia.

Fig. 12. Longleaf pine–wire-grass savannah at Piney Bottom Creek, North Carolina. These fire-maintained communities have high plant and animal diversities.

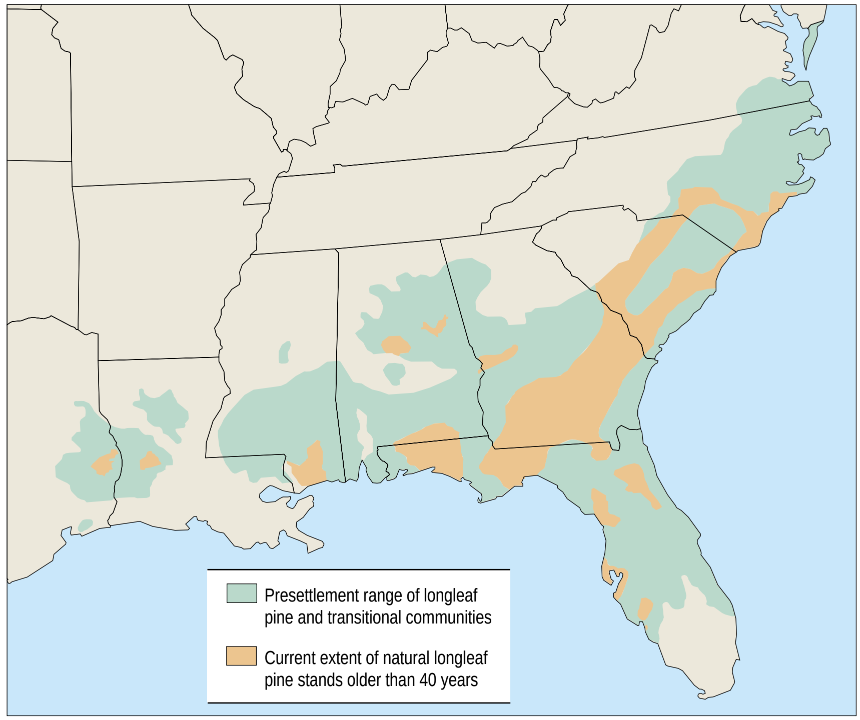

Fig. 13. Former and current extent of natural longleaf pine stands in the southeastern United States (former extent taken from Ware et al. 1993; current extent from Outcalt and Outcalt 1994) Current extent includes old-growth longleaf pine stands and natural second-growth stands older than 40 years.

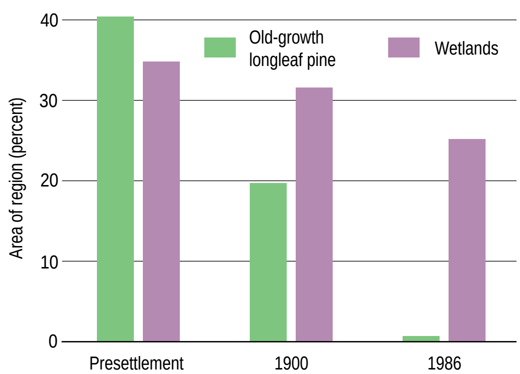

Fig. 14. Percentage of the southeastern Costal Plain composed of longleaf pine and various wetland communities in presettlement time (pre-1880), 1900, and 1986 (redrawn from Noss 1989, as adapted from tabular data in Ware et al. 1993).

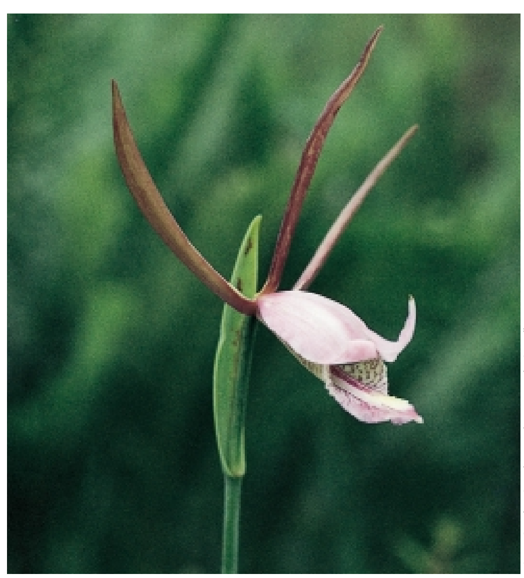

Fig. 15. Spreading pogonia, a native orchid of longleaf pine–wire-grass communities in the Carolina Sandhills, Fort Bragg, North Carolina.

with just 3% surviving as old-growth habitat, a loss comparable with or exceeding that of many of the other unique communities in North America (Noss 1989; Figs. 13 and 14). The dry longleaf pine–turkey oak stands of the sandhills are the most poorly protected areas of this endangered ecosystem (Stout and Marion 1993).

Species that inhabit longleaf pinelands exhibit a high incidence of rarity and endemism. The longleaf pine–wire-grass community includes 191 species of rare plants (Figs. 15 and 16). Although pine communities on the Atlantic Coastal Plain are more diverse and contain a greater number of rare plants, the west Gulf Coastal Plain also has high

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Fig. 16. Meadow beauty in the longleaf pine–wire-grass communities in the Carolina Sandhills, McBee, South Carolina.

endemism, with 39 endemic species (Bridges and Orzell 1989). The southeastern pineland community harbors large numbers of federally listed species: 18 plants, 4 reptiles, 4 birds, and 1 mammal, as well as 100 candidates for federal listing (Noss et al. 1995). In addition, the pinelands serve as a major corridor for a large number of migratory birds that winter in the West Indies and South America (Stout and Marion 1993), and they support 170 species of reptiles and amphibians (Dodd 1995a). High percentages of these reptile and amphibian species are imperiled (endangered, threatened, or declining): 22% of the salamanders, 15% of the frogs, 34% of the turtles, 31% of the lizards, and 19% of the snakes fall in this category (Dodd 1995a; Fig. 17).

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Fig. 17. Florida pine snake in the sandhills of the Katherine Ordway Preserve—Swisher Memorial Sanctuary.

Lightning fires, occurring at about 1- to 3-year intervals throughout the area, were carried over large areas by wire-grass and pine duff and were stopped only by excessive moisture or abrupt changes in topography. Historically, 10%–30% of the southeastern pinelands burned each year (Ferry et al. 1995); these frequent fires reduced litter accumulation and invasion by competing woody species. Pine seedlings and many of the grasses and forbs present in longleaf pine communities are shade-intolerant, and many require bare mineral soil and reduced competition for germination and early growth. Longleaf pine has several adaptations to minimize fire injury and a large annual needle cast that provides good fuel for future fires (Stout and Marion 1993). The reduction of litter accumulation is essential for the survival of small, rare herbaceous species such as the unique Venus flytrap.

By the time European explorers and settlers arrived in this region, Native Americans had already been augmenting the natural lightning-caused fire regime with annual burning. Set in fall and winter, these fires were used to drive game and improve browse. Early settlers also used fire in winter to improve forage for their livestock, which roamed freely in the forested land.

The longleaf pine forest remained largely intact until the mid-seventeenth century, when the Naval stores industry (that is, products such as turpentine or pitch, originally used to caulk the seams of wooden ships) started to develop in Virginia and then reached its full development in North Carolina in the mid-eighteenth century. Demand then turned to timberland, and despite warnings from late nineteenth-century foresters concerned with regeneration, much of the old-growth forest was cut by the 1920's (Ware et al. 1993).

With much of the timberland being converted to agriculture and much of the wire-grass understory disturbed and fragmented by logging roads and fields, the era of unrestricted ground fires ended. In the absence of fire, other species of pines and woody plants invaded, shading out the regenerating longleaf pine and the sun-loving herbaceous layer. The introduction of livestock also contributed to the end of regeneration by longleaf pine; the nonresinous, carbohydrate-rich meristems of longleaf pine seedlings became favorite livestock forage. In the mesic regions along the coast, extensive areas of longleaf pine were cut, drained, and converted to commercial pine plantations. Finally, the initiation of government-sponsored fire suppression in the 1920's completed the demise of fire-maintained longleaf pinelands in all but a few locations. By 1946 the range of longleaf pinelands had decreased to one-sixth of their former extent, and today only 14% of the original total remains (Frost et al. 1986).

Much of the remaining 2 million hectares of longleaf pine are fragmented and located near developed areas. Winter burning can actually promote woody invasion of the wire-grass understories, but summer burning (the natural fire regime) is considered hazardous near human property. Prescribed burning relies on firebreaks and roads, which further fragment the herbaceous understory and alter local hydrology (Noss 1989). Even though some rare native species respond to other types of disturbance, fire is the most universally important disturbance (Hardin and White 1989).

Of the animals dependent on longleaf pinelands, the best known is the red-cockaded woodpecker, a federally listed species unique for its use of live old-growth or mature second-growth pine trees for cavity excavation (Costa and Walker 1995). The red-cockaded woodpecker is the prime cavity builder in an environment largely free of snags and natural cavities. This species has declined with the loss of longleaf pine habitat; however, intensive management has stabilized several populations (Costa and Walker 1995). Bachman's sparrow, federally listed as threatened, nests in the wire-grass tussocks. The fox squirrel is dependent on the longleaf pine for forage in late summer (Ware et al. 1993). The gopher tortoise, a species whose populations have declined by 80% in the past 100 years (Auffenberg and Franz 1982), is a keystone species in longleaf pine savannahs—more than 300 species of invertebrates and 65 species of vertebrates use burrows dug by gopher tortoises, the only species that creates this microhabitat (Dodd 1995a). Recent regional trends are not available for this species. A study in Florida showed that gopher tortoise populations had increased on one study site, decreased on another, and remained stable on three others (data from 1987 to 1988 compared with 1978 to 1979; McCoy and Mushinsky 1992).

Carolina Bays

Carolina bays are isolated shallow basins with an elliptical shape and oriented in a northwest to southeast direction. Bays are distributed from New Jersey to northern Florida (Sharitz and Gibbons 1982; Richardson and Gibbons 1993). Estimates of how many of these bays originally existed in the Southeast vary because insufficient inventories have been completed and because development has altered some bays beyond recognition. Recent calculations, however, indicate that there were between 10,000 and 20,000 Carolina bays (Richardson and Gibbons 1993), with an estimated 4,000 bays once occurring in South Carolina (Bennett and Nelson 1991). About 80% of the bays are in North Carolina and South Carolina (Crisman 1992; Fig. 18).

The size of bays varies; for example, length varies from 50 meters to 8 kilometers (Lake Waccamaw in southern North Carolina). The substrate can be clay, sand, or organic material (Richardson and Gibbons 1993). Hydroperiod ranges from short-duration flooding, where evapotranspiration causes complete drying, to sites with permanently saturated soils, to sites with permanently standing water (Sharitz and Gibbons 1982). Carolina bays depend mostly on rainwater for hydrology and nutrients, although some evidence indicates that the hydrology of some bays may have connection with groundwater (Sharitz and Gibbons 1982). This dependence on precipitation results in large fluctuations in water levels during a year and in variation between years (Sharitz and Gibbons 1982), causing the year-to-year variation in composition and biomass observed in Carolina bay communities (Sutter and Kral 1994). Like many southeastern Coastal Plain ecosystems, most Carolina bay communities historically had regularly occurring fires, but fire regime varied with hydroperiod and vegetation.

Given this range of substrates, hydrology, and fire history, bays are, not surprisingly, biologically variable. Richardson and Gibbons

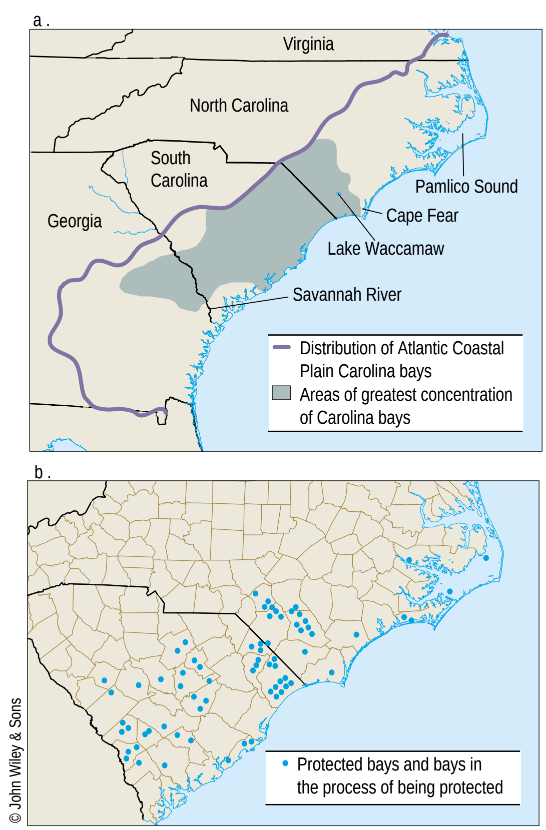

Fig. 18. Distribution and protection of Carolina bays. a) South Atlantic Coastal Plain showing distribution of Carolina bays larger than 246 meters in length (based on Richardson and Gibbons's 1993 interpretation of a map in Prouty [1952]). b) Carolina bays that have been protected or are in the process of being protected as of June 1995 (data for South Carolina are from Bennett and Nelson [1991]; data for North Carolina are from M. Schafale, Natural Heritage Program, Raleigh, North Carolina, unpublished data).

(1993) listed plant communities that occur in bays: pine forest or savanna, herbaceous marsh, shrub bog, deciduous forest dominated by blackgum, evergreen bay forest, and pondcypress swamp with herbaceous understories. Bennett and Nelson (1991) added xeric sandhill scrub, oak–hickory forest, swamp forest, depression meadow, shrub border, and open-water lake.

Sutter and Kral (1994) estimated that nonalluvial wetlands (of which Carolina bays are a major portion) support more than one-third of the rare plants that occur in the Southeast. Bennett and Nelson (1991) listed 23 species of rare, threatened, or otherwise noteworthy plants in bays in South Carolina.

Carolina bays represent a major portion of the freshwater habitat in the southeastern Coastal Plain. Animals that depend on bay habitat include amphibians, the American alligator, freshwater turtles, snakes, and birds (Sharitz and Gibbons 1982). Because of their fluctuating water levels, few bays can support fishes, but bay lakes do support permanent fish populations (Sharitz and Gibbons 1982). Some bays that lack fish populations are important predator-free breeding sites for amphibians. Several animal species are endemic to particular bays; Lake Waccamaw, for example, supports at least two and possibly four endemic fish species and three endemic mollusk species.

Carolina bays are threatened by ditching for agriculture (the most common disturbance), silviculture, and grazing; changes in local and regional hydrology; development for recreation, residence, and industry; and fire suppression (Sutter and Kral 1994). Bennett and Nelson (1991) surveyed 2,651 bays (Fig. 19) in South Carolina and found that 97% had undergone some form of alteration, and 81% had experienced two or more kinds of human disturbance. Out of the 4,000 original bays in South Carolina, they estimated that 400–500 are still relatively intact. Wetland regulations have protected many privately owned bays on the Coastal Plain, but fewer than 2,000 hectares of this community are protected in North Carolina (Richardson and Gibbons 1993).

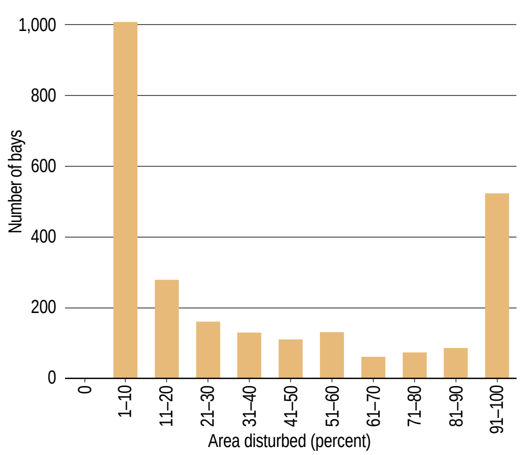

Fig. 19. Number of Carolina bays negatively affected (percent of surface area disturbed) by human factors. Percentages based on surveys of 2,651 Carolina bays in South Carolina (redrawn from Bennett and Nelson 1991).

Pocosins

The word *pocosin* comes from an Algonquin word meaning "swamp-on-a-hill" (Tooker 1899), referring to the position of this wetland community in upland interstream areas. Pocosins are freshwater wetlands dominated by a dense cover of broad-leaved evergreen shrubs or low-growing trees with highly organic soils developed in areas of poor drainage (Sharitz and Gibbons 1982; Christensen 1988). The soils are low in pH and available nutrients, with phosphorus often a limiting factor (Richardson and Gibbons 1993). Vegetation is separated from the underlying mineral soils by the organic layer and is isolated from runoff because of its landscape position in broad divides and flats without much watershed to feed water onto the site. In extreme circumstances, the only nutrients available to plants come from rainfall.

The most nutrient-limited pocosins are those where peat is deep (more than 1 meter [Christensen 1988]), which results in lower productivity and shorter vegetation (less than 6 meters); these areas are commonly referred to as short or low pocosin. Where peat is shallower (0.5–1 meter deep), vegetation is taller, and the area is referred to as tall or high pocosin. High pocosin usually surrounds low pocosin (Richardson and Gibbons 1993). Short pocosin develops from tall pocosin because peat accumulation eventually prevents roots from reaching the mineral soil, a condition that continues until fire burns the peat so that mineral soils are accessible again (Christensen 1988).

Pocosins are fire-maintained ecosystems. In addition to being adapted to flooded and low-nutrient conditions, plants in pocosins either tolerate fire or depend on it to complete their life cycles (Sharitz and Gibbons 1982). Without fire to maintain or generate openings in the dense shrubs and to open serotinous fruits, some species cannot continue to persist. Vegetative production in pocosins is highest in the first two growing seasons following a fire (Christensen 1988).

Several plant species depend on pocosin habitat, including whitewicky, arrowleaf shieldwort, spring-flowering goldenrod, and roughleaf yellow loosestrife. Others, such as the Venus flytrap, dwarf witchalder, sweet pitcherplant, and whitebeaked rush, depend at least in part on pocosins or associated habitats (Richardson 1983).

No vertebrate animals are endemic to pocosins, but for many species pocosins are key habitat and refuge from the development of the surrounding landscape (Richardson and Gibbons 1993). Although information on fauna remains limited, Clark et al. (1985) found 41 species of mammals inhabiting 12 pocosin and Carolina bay sites in North Carolina.

Pocosins also store and regulate fresh water for regional ecosystems (Richardson and Gibbons 1993). In addition, their other valuable functions are input of organic matter to streams and rivers and filtering of dissolved nutrients and suspended materials, thereby reducing eutrophication (Richardson 1983).

The presettlement distribution of pocosins has been estimated at 1.2 million hectares (Richardson 1983). Of the 907,933 hectares of pocosin that existed in North Carolina in 1962, by 1980, 33% had been entirely developed, 36% had been partially developed, and only 31% (281,180 hectares) remained in a more or less natural state (Richardson et al. 1981). From 1980 to 1989, the amount of surviving area that was protected increased from 5% to 22% (Richardson and Gibbons 1993). In 1989, about one-third of the unprotected pocosin area was owned by major timber companies; other large landholders included corporate agriculture (14%) and federal and state agencies (18%; Richardson and Gibbons 1993; Fig. 20). Alteration and conversion of pocosins have been primarily due to timber production, agriculture, and peat mining. Recent changes in the enforcement of the Clean Water Act in North Carolina have reduced the amount of development in pocosins (Richardson and Gibbons 1993).

Carnivorous Plants

The Southeast possesses the highest diversity of carnivorous plants in the world (Fig. 21). As many as 20 species occur in a single site, and 54 species in five genera and three families occur across the region (Gibson 1983). These plants obtain nutrients from animals, particularly insects, via elaborate adaptations, such as sticky leaves, hollow tubular leaves, and traps. Vast wet meadows once covered hundreds of hectares on the outer Atlantic Coastal Plain and Gulf Coastal Plain, with smaller hillside seepage bogs inland. Gibson (1983) reported two centers of diversity, one in North Carolina and the other in Alabama (Fig. 22). The highest diversities are found in regions where wetlands (longleaf pine savannas and pocosins) are most numerous and closest together. However, there has been a dramatic loss of area for these habitats—less than 3% remains as degraded habitat, and less than 1% remains as pristine habitat (Folkerts 1982).

As sites are lost, the isolation of carnivorous plant wetlands is increasing, which may cause species to fail to disperse among sites. Gibson (1983) described the loss of area and increased isolation as factors that will cause a collapse of carnivorous plant diversity in these habitats. The most important causes of loss of habitat have been fire suppression and the draining of wetlands for agriculture and forest plantations. Other commercial effects are flooding caused by construction of fish ponds and changes in water quality due to fertilizer runoff (plant carnivory is an adaptation to low-fertility soils). In addition, private and commercial plant collectors seek out the rarest species. Over the last 100 years such collecting has removed millions of plants; a new collection pressure has come from the use of the Venus flytrap as a source of an herb medicine, Carnivora, produced in Europe.

The number of populations of this unique and narrowly restricted endemic plant has decreased from 21 to 12 in the last century (Figs. 23 and 24). The collection of the Venus flytrap on public land is now regulated by the state of North Carolina.

Examples of ongoing population loss come from 2 federally listed species of pitcher-plants. Jones' pitcher-plant has declined from 26 to 10 populations, all of which are small and 8 of which occur on private land (Endangered Species Technical Bulletin 1988). Likewise, the Alabama pitcher-plant has declined from 28 to 12 populations, of which only 4 are significant (Endangered Species Technical Bulletin 1989).

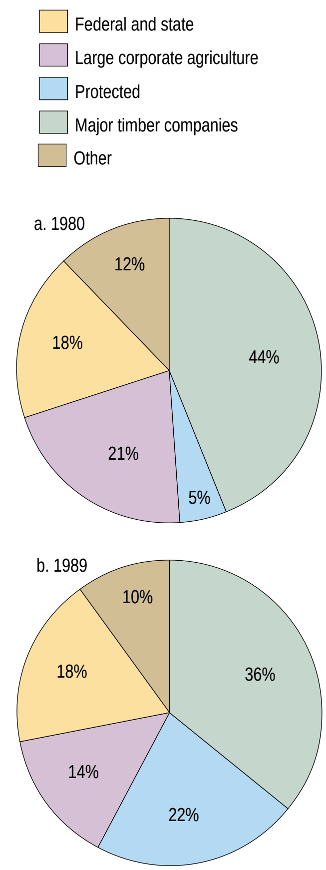

Fig. 20. Ownership patterns, by percent, of North Carolina pocosin wetlands in a) 1980 and b) 1989 (redrawn from Richardson and Gibbons 1993). © John Wiley & Sons

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Fig. 21. Yellow pitcher-plants in a seepage bog in the North Carolina Sandhills. The southeastern Coastal Plain is a world center for the diversity of carnivorous plants, with 54 species in 5 genera and 3 families. Carnivory provides an added source of plant nutrients on sandy sites that are often acidic and nutrient-poor. Diversity of carnivorous plants, as well as other herbaceous species, is promoted by fire in these habitats.

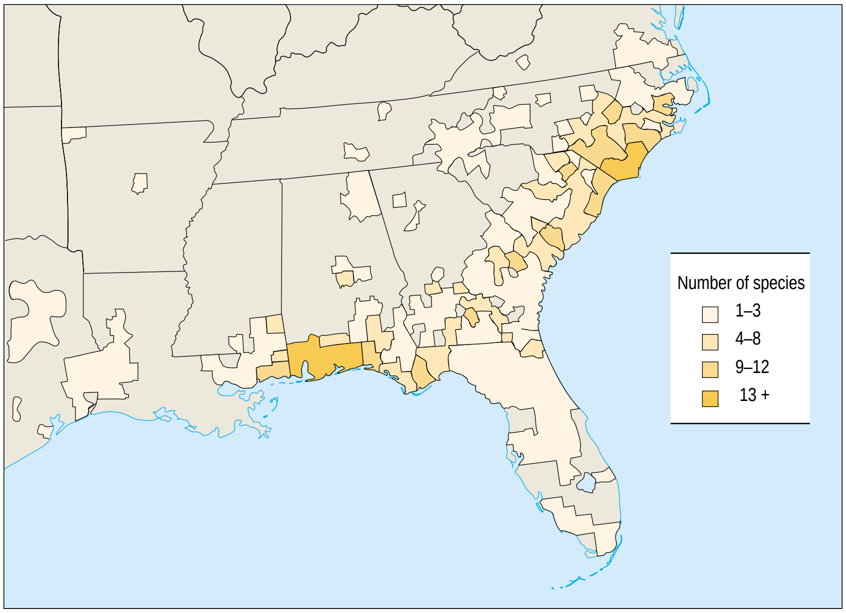

Fig. 22 . Two major centers of diversity in the carnivorous plant community: the Atlantic Coastal Plain and the Gulf Coastal Plain. Data are from numerous sources, including herbarium records (Gibson 1983).

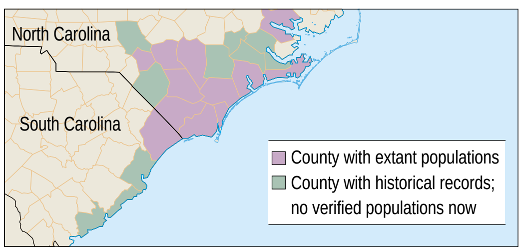

Fig. 23. Distribution of Venus fly-trap in the Carolinas (redrawn from Boyer 1995). Only 12 of 21 historical county locations are extant.

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Fig. 24. The Venus flytrap is a carnivorous plant whose image is known the world over but which is restricted in the wild to an extremely small part of North Carolina and South Carolina. This plant, which is subject to exploitation, depends on habitat protection and fire management.

Atlantic White-Cedar Swamps

Atlantic white-cedar swamps are unique communities adapted to variable hydrological regimes, fire, and acidic, nutrient-poor peat soils (Levy 1987). Fire removes competitive vegetation and clears the seedbed for white-cedar regeneration (Laderman 1989). White-cedar, though, is not a fire-resistant species and can be severely damaged in prolonged hot fires. Although white-cedar is not tolerant of prolonged flooding, brief, frequent flooding reduces competing species and is essential for white-cedar reproduction. Thus, white-cedar stands require frequent, light fires in the dry season and waterlogged soils subject to a variable hydroperiod (Laderman 1989).

Because of the difficulty and expense associated with exploiting these communities, white-cedar stands often represent some of the only forested land in a region of intense agricultural and developmental pressure. Atlantic white-cedar wetlands provide habitat and essential cover for many species, including black bear, deer, rabbits, and other fauna (Laderman 1989). Unique species occur as well, including Hessel's hairstreak, a butterfly that feeds exclusively on Atlantic white-cedar (Laderman 1989). The diversity of bird species is relatively high in Atlantic white-cedar swamps (Terwilliger 1987).

Much of the original Atlantic white-cedar community was destroyed during European colonization and the timbering and draining for agriculture that occurred during the last two centuries. Road construction and the ditching and damming of natural waterways continue to diminish this habitat, as does suburban encroachment, agricultural and industrial runoff, and pollution. Those white-cedar stands not protected by law are threatened by these continuing activities (Laderman 1989).

Historically, Atlantic white-cedar was found in the South in a nearly continuous band from southeastern coastal Virginia to the interior sandhills region of Georgia, and from the Florida Panhandle across the Gulf of Mexico coast to Mississippi (Frost 1987). Now Atlantic white-cedar swamps are restricted to inaccessible or protected freshwater wetlands in small, isolated stands (Laderman 1989). Drainage, development, and logging have reduced Atlantic white-cedar to 10% of its original extent (Frost 1987).

Barrier Island Communities and Maritime Forests

The Southeast supports over 200 individual barrier islands with a total area of over 610,000 hectares (Bellis and Keough 1995). The ecosystems (Fig. 25) of these islands are diverse and dynamic, a product of regional climate, geomorphology, local sediment deposition, and the forces of ocean currents, tides, wind, salt spray, erosion, and violent ocean storms (Bellis 1992; Stalter and Odum 1993; Bellis and Keough 1995). The islands are grouped into five geographical categories: the mid-Atlantic region, extending from New Jersey to Cape Hatteras, North Carolina; the Sea Islands, bordering the coasts of South Carolina and Georgia; the Florida Atlantic; the eastern Gulf of Mexico coast; and the Louisiana–Texas Gulf of Mexico coast (Stalter and Odum 1993).

Human activities have only had a major effect on the barrier islands in the past 50 years (Fig. 26). Eighteenth- and nineteenth-century settlements were small, scattered, and difficult to reach. Most activities were confined to forestry, livestock grazing, and subsistence agriculture, except in the Georgia and South Carolina Sea Islands, where cotton and rice plantations were widespread. The construction of bridges and causeways and the improvement of transportation in the early part of this century brought new opportunities for recreation, tourism, and second-home development. Development has meant the construction of jetties and sea walls, filling and draining of marshes, and extensive dune stabilization and beach nourishment programs, all of which obstruct the natural fluctuations of the barrier island communities. Despite limited fresh water and the constant threat of storm damage, development continues at an accelerating pace (Stalter and Odum 1993). Barrier island development in the Southeast has increased more than 300% in the past 50 years (Johnson and Barbour 1990), and coastal Florida's development proceeds at a rate nearly twice that of the entire Atlantic and Gulf of Mexico coasts combined (Johnson and Barbour 1990). Although there are stretches of protected barrier island beaches and dunes and intact salt- and freshwater marshes, close to half of the area of these communities is estimated to have already been lost (Noss et al. 1995).

Development, of course, has many effects. Beach traffic disturbs nesting birds and sea turtles, compacts the soil, and disrupts dune-building activities. Jetties, sea walls, inlet stabilization, and artificial dunes disrupt normal overwash activities, altering normal dune development and increasing erosion in some areas and sand deposition in others. Development within the foredune zone and forest clearing destroy natural protective barriers to salt spray and wind damage. Pollution of marshes, estuaries, and creeks is a common result of inputs of treated and untreated sewage, fertilizer runoff from developments such as golf courses, and numerous contaminants from marinas, fish-processing plants, highways, and small industries (Stalter and Odum 1993). Finally, fragmentation of vegetation interferes with natural migration patterns.

Experience with severe storm damage on coastal structures has modified development activities to some extent. Today, setback requirements in effect in many areas prohibit the destruction of the foredunes and reduce effects on beach areas. Existing structures, however, still require protection from beach migration, as well as regular, costly, beach nourishment projects (Johnson and Barbour 1990). About one-third of the barrier islands lining the Atlantic and Gulf of Mexico coasts have been protected by being set aside as parks, wildlife management areas, and national seashores (Stalter and Odum 1993). Areas that are open for development, however, are largely at risk for continued severe habitat degradation and other environmental losses. Most of the Atlantic coast of Florida is unprotected and very little natural coastline remains.

Maritime communities have decreased in areal extent since settlement, but the magnitude is known only for local areas. For example, coastal wetlands around Tampa Bay have decreased by 44% (Johnston et al. 1995). From 1950 to the present, the area of coastal wetlands along the Gulf of Mexico decreased by 20%–35% (Johnston et al. 1995); the largest losses were in Louisiana, where coastal impoundments flooded wetlands (Fig. 27). In general, freshwater wetlands have decreased to a much greater extent than estuarine wetlands. In 1982 the Coastal Barrier Resources Act restricted the use of federal funds for development of barrier islands. An extensive monitoring system has shown that the area of undeveloped barrier islands has been stable since that law was passed (Williams and Johnston 1995).

Bellis and Keough (1995) estimated that 39,000 hectares of maritime forest occurred in

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Fig. 25. Sea oats dominate the primary dunes along the North Carolina coast.

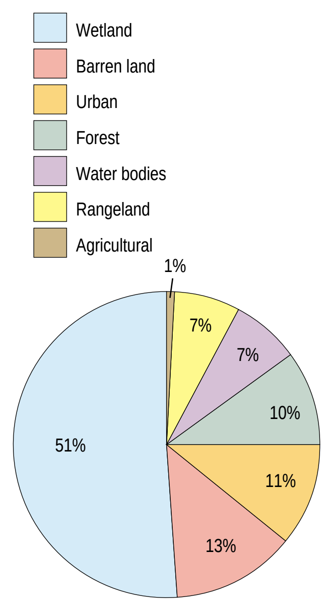

Fig. 26. Barrier island land use (redrawn from Stalter and Odum 1993; data from Lins 1980).

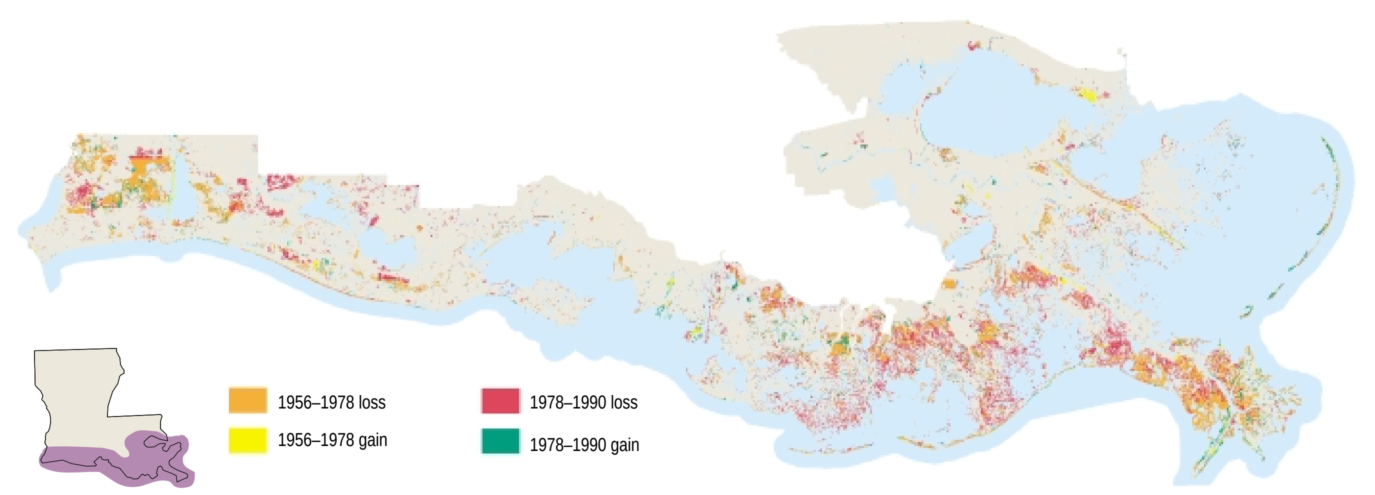

Fig. 27. Coastal land loss and land gain in Louisiana, 1956–1990 (Johnston et al. 1995).

North Carolina, Georgia, and Florida, the three states with the best inventories. This represents an unknown fraction of the original extent of these forests. About half of the remaining forests are unprotected and likely to be developed within the next decade (Bellis and Keough 1995; Table 9). The degree of human disturbance and changes within the small forest fragments that remain (for example, edge effect and the fact that fragments may not be large enough to support a population big enough to convey long-term persistence) produce declines in the numbers and species of many animals (Gaddy and Kohlsaat 1987; Bellis and Keough 1995).

Several investigators noted the inadequacy of existing data for detection of trends. Bellis and Keough (1995) suggested the need for a complete survey and assessment of maritime forests. Besides effects of development and nonindigenous species, maritime communities will probably be influenced by sea-level rise and drawdown of freshwater supplies (Bellis and Keough 1995). Daniels et al. (1993) modeled the influence of sea-level rise on endangered species in South Carolina and showed that 52% of the regionally endangered species were found within 3 meters of current mean sea level and that several scenarios of sea-level rise would drastically reduce the habitat for these species.

Overgrazing is also a problem on barrier islands, not only because of a large white-tailed deer population but also because of the large numbers of feral animals introduced to the islands, including horses, cattle, goats, pigs, and sheep (Stalter and Odum 1993). Eradication of some of the larger feral species has been successful on some islands, but other introduced animals, especially feral dogs and cats, negatively affect small mammal populations. Other introduced species include European rats and nutria (Stalter and Odum 1993).

Large numbers of migratory and nesting bird species are found on barrier islands (Stalter and Odum 1993); for example, 350 species have been recorded on barrier islands in North Carolina alone (Parnell et al. 1992). Coastal marshes are critical to overwintering populations of many waterbirds. In addition, migration routes of many raptor species include southeastern barrier islands. Neotropical migrants use the islands as a point of departure and arrival in their travels to and from their winter habitats in the tropics (Stalter and Odum 1993).

Many birds have been negatively affected by development and human encroachment. Species that nest in bare sand can be disturbed by pedestrian and off-road vehicle traffic and by the construction of artificial dunes. Harrington (1995) reported that for 27 species of eastern shorebirds, 12 had stable populations, 1 was increasing, and 14 were decreasing. Surveys initiated off the North Carolina coast in the early 1970's tracked the fluctuations in nesting bird populations (Parnell et al. 1992; Table 10). Eight species were increasing strongly (brown pelican, cattle egret, white ibis, glossy ibis, laughing gull, herring gull, royal tern, and Sandwich tern), three were increasing (yellow-crowned night-heron, great black-backed gull, and caspian tern), four were declining (gull-billed tern, common tern, least tern, and black skimmer), and seven were presumed stable. Some of the species have even shifted locations; Parnell et al. (1992) suggested that cutting of coastal swamps during the last 50 years resulted in movement to the estuaries. Further, creation

Table 9. Development and maritime forests on the Southeast's Atlantic Coastal Plain (from Bellis 1992). NA = data not available.

State	Shoreline (kilometers)	Undeveloped maritime forest (hectares)	Developed maritime forest (hectares)	Undeveloped, unprotected maritime forest (percent, 1992)
Florida	690	NA	NA	NA
Georgia	155	156,165	21,418	35
South Carolina	295	68,740	45,000	71
North Carolina	480	15,558	NA	55
Virginia	225	NA	NA	NA

of new habitat from dredged material may have caused populations to shift from one estuary to another.

Stalter and Odum (1993) listed nine endangered species of birds that are wholly or partially dependent on habitat on southeastern barrier islands: whooping crane, Eskimo curlew, bald eagle, Arctic peregrine falcon, eastern brown pelican, Cape Sable seaside sparrow, Bachman's warbler, Kirtland's warbler, and red-cockaded woodpecker. These species use the barrier islands in a variety of ways: nesting (five species), migration (four species), wintering (five species), feeding (seven species), and resting–roosting (seven species). Stalter and Odum (1993) attributed population losses in these species to development (direct loss of nesting, resting, and foraging habitat), dredging and filling of marshlands (loss of community structure and composition used by the birds), pollution, and direct disturbance on recreational beaches.

Five species of sea turtles are found in the open ocean and coastal waters of the Southeast, and all nest on open beaches: the green sea turtle (status: endangered/threatened; U.S. Department of Commerce 1994), the hawksbill (endangered), Kemp's ridley (endangered), the leatherback (endangered), and the loggerhead (threatened). Sea turtles are difficult to census in open waters and, because of the concentration of female turtles nesting on the beach strand and the apparent faithfulness of their return to specific beaches, the number of nesting females is considered the single best indicator of population trends (Committee on Sea Turtle Conservation 1990). The Kemp's ridley nests annually, but the other species nest less regularly. Long-term data sets (that is, over a decade of observations) are essential to detecting trends (Committee on Sea Turtle Conservation 1990). The dependence of sea turtle species on the narrow beach strand also makes them vulnerable to a host of human-caused problems, including beach development and recreation, artificial lighting (which disorients hatchlings), and increases in nest predators such as raccoons. Recently, federal law has mandated that shrimp trawlers use turtle exclusion devices, which should decrease mortality in a critical life stage for reproduction (Committee on Sea Turtle Conservation 1990).

Population estimates are available for only two of the five species of sea turtles (U.S. Department of Commerce 1994): 20,000–28,000 loggerheads and 400–500 green sea turtles nest in the United States. Although the number of nesting loggerheads has declined by 3% annually at a site in Georgia and by 26% during the 1980's at a site in South Carolina, it has increased at several sites in Florida

Table 10. Trend data for nesting coastal waterbirds in North Carolina (from Parnell et al. 1992).

Species	Pre-1900's	Early 1900's	Current status	Current trend
Black-crowned night-heron	Rare	Common	Common	None
Black skimmer	Unknown	Abundant	Common	Declining
Brown pelican	Unknown	Absent	Abundant	Increasing
Caspian tern	Unknown	Absent	Uncommon	Increasing
Cattle egret	Absent	Absent	Abundant	Increasing
Common tern	Unknown	Abundant	Common	Declining
Forster's tern	Absent	Absent	Common	None
Glossy ibis	Absent	Absent	Common	Increasing
Great black-backed gull	Absent	Absent	Common	Increasing
Great blue heron	Unknown	Common	Uncommon	Unknown
Great egret	Abundant	Rare	Common	None
Green heron	Unknown	Common	Sparse	None
Gull-billed tern	Absent	Rare	Common	Declining
Herring gull	Absent	Absent	Common	Increasing
Laughing gull	Absent	Common	Abundant	Increasing
Least tern	Abundant	Sparse	Common	Declining
Little blue heron	Common	Abundant	Common	None
Royal tern	Common	Abundant	Abundant	Increasing
Sandwich tern	Unknown	Sparse	Common	Increasing
Snowy egret	Unknown	Rare	Common	None
Tricolored heron	Common	Common	Common	None
White ibis	Absent	Absent	Common	Increasing
Yellow-crowned night-heron	Rare	Rare	Sparse	Increasing

(Committee on Sea Turtle Conservation 1990; Dodd 1995b; Fig. 28). Summed across the Southeast, loggerheads increased from 1982 to 1990 and decreased from 1990 to 1993 (Dodd 1995b), although the recent decline has been relatively mild, leaving the species at higher levels than in the early 1980's. A recent review concluded that the overall status of loggerhead population size was stable (U.S. Department of Commerce 1994). This study also concluded that there was inadequate data to report an overall trend in green sea turtle populations, but numbers at one Florida site had increased from 1971 to 1989 (Fig. 28), and the species is presumed to be recovering. The green sea turtle was drastically reduced by fishing (it was served in turtle soup) during the early 1900's.

At one study site in Mexico, Kemp's ridley is presumed to have declined sharply from 1947 to 1990, to 1% of original levels (Committee on Sea Turtle Conservation 1990). Data collected at that site from 1977 to 1990 suggested a continued but much less drastic downward trend (Fig. 28). Very few hawksbills and leatherbacks nest in the United States, and data are inadequate for precise statements of trends of these species, although expert opinion holds that the hawksbill is declining (U.S. Department of Commerce 1994).

Central and South Florida

Everglades

Nowhere in the Southeast does the conflict between natural diversity and the needs of a growing human population occur on such a large scale as in the Everglades of south Florida (Davis and Ogden 1994b). The

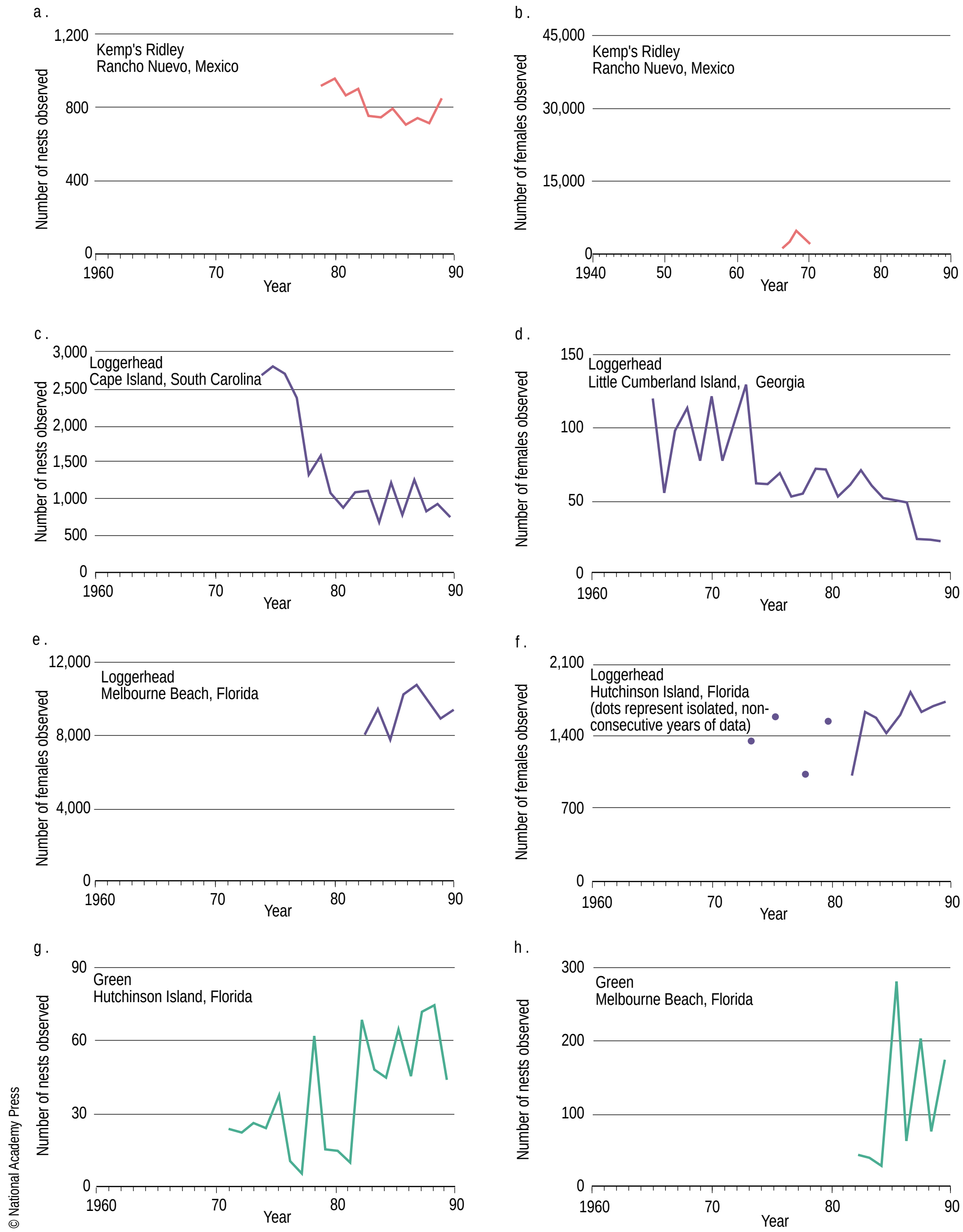

Fig. 28a-h. Trends in sea turtle populations (from Committee on Sea Turtle Conservation 1990).

Everglades consist of a broad river of sawgrass with pools of open water and scattered islands of shrubs and trees. Historically, the system extended from Lake Okeechobee to Florida Bay.

The Everglades are bordered by the Everglades Agricultural Area to the north and west and by urbanization on Florida's east and west coasts. The flow of water in the northern part of the Everglades system, between Lake Okeechobee and Everglades National Park, is regulated in a series of impoundments to control flooding and provide water for agriculture and human populations. The amount, seasonal variation, and chemical composition of the water supply is critical to the ecosystems of the Everglades.

Everglades National Park has been called the first U.S. national park established for its biological diversity rather than for its scenic grandeur, for it was the preservation of the tremendous diversity of wading birds and other wildlife that was prominent in the founding documents. Everglades National Park, however, protected less than 20% of the sawgrass marsh for which the Everglades are named, and the

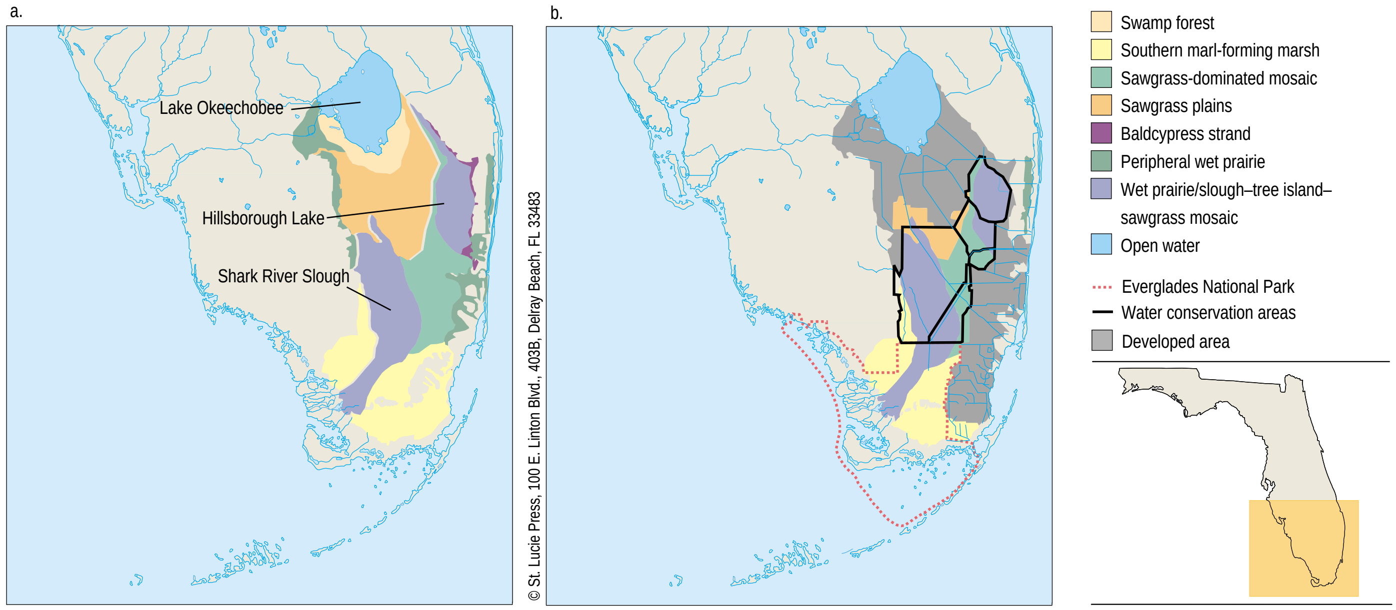

Fig. 29. a) Former (around 1900) and b) current (1990) extent of Everglades vegetation (redrawn from Davis and Ogden 1994a,b).

area protected is the lowest portion of the watershed and thus is vulnerable to upstream manipulation of water supply (Davis and Ogden 1994a). Although the full extent of the Everglades *river of grass* was one million hectares (Fig. 29), 50% of this original wetland area has been drained and used for agriculture and development. The balance, 30%, is within impoundments of the South Florida Water Management District (Davis and Ogden 1994a).

A mosaic of unique and interacting ecosystems (Fig. 30) exists in the Everglades (Gunderson and Loftus 1993): ponds, sloughs, sawgrass marshes, wet prairies on peat (including three types), wet prairies on marl, bayhead swamp forests, pond-apple forests, willow heads, baldcypress forests, and hardwood hammocks. Two critical variables in this mosaic are hydrology and fire regime, although tropical storms, sea-level rise, habitat fragmentation, alterations to nutrients in drainage waters, and invasions by nonindigenous species (including one tree species, Australian melaleuca, that greatly influences ecosystem function in the Everglades) are also important (White 1994).

Since 1900 water flow to Everglades National Park has followed eight different hydrological regimes under human influence (Davis and Ogden 1994b). The dominant theme from 1920 until increased attempts at restoration in 1985 was reduction in the extent and duration of inundation in the park (producing a secondary effect of lower relative elevation of sites through higher oxidation rates of organic muck), the pooling of waters behind levees north of the park, the loss of transitional glade communities, a change from attenuated to pulsed flows, and a reduction of freshwater flows to Florida Bay (Fennema et al. 1994; Light and Dineen 1994).

Over the same period, wading bird populations within the park decreased to 10%–20% of original densities (Bennetts et al. 1994; Davis and Ogden 1994a; Light and Dineen 1994; Ogden 1994). In addition, the Everglades now have no nesting colonies of white ibis, have fewer than 1,000 pairs of great egrets, and fewer than 500 pairs of snowy egrets (Light and Dineen 1994). Robertson and Frederick (1994) noted that Everglades National Park was once a source of wading birds for other areas but since 1900 has become a sink for birds produced elsewhere. The declines within the park were accompanied by spatial shifts in the populations within the park (Ogden 1994), as well as shifts for some species to areas outside the park. The Everglade snail kite would seem particularly vulnerable because of its restricted distribution,

Fig. 30. Relatively low elevations and underlying rock formations produce the mosaiclike nature and abrupt boundaries of many plant communities in the Everglades.

small and fluctuating population size, and dependence on a single food item, the apple snail.

The changes to the wading bird populations are a result of decreases in the extent of the wetland foraging habitat (Ogden 1994), particularly of the early dry season habitat (Davis et al. 1994). With this loss in area there were also decreases in the connectivity, heterogeneity, and total productivity of the sawgrass marsh, which already has one of the lowest productivities for wetlands (Davis et al. 1994). These changes are well established and universally associated with changed hydroperiod. Robertson and Frederick (1994) noted, however, that there are relatively few good quantitative studies, that data on animals other than birds are lacking, and that uncertainty exists about the specific ecological mechanism behind the trends (that is, about the availability and productivity of prey for the wading birds and how these populations are affected by hydroperiod). Loftus and Eklund (1994) noted not only the widespread report of downward trends in fish populations but also the lack of consistent long-term studies of these populations. They also described the problem of detecting trends given a lack of understanding of natural variability and that some populations may shift spatially (thus, a local decline might not be a global decline).

Davis et al. (1994) produced an exemplary study of landscape change in the historical Everglades. They depicted change on two scales. First, they used historical vegetation maps to reconstruct the predrainage landscape of the Everglades and compared this with a modern vegetation map for the area. Next, they mapped plant communities in greater detail on 25 randomly selected study areas, each a square mile (259 hectares), by using imagery from 1965 to 1971 and from 1984 to 1987. On the regional scale, three of seven physiographic landscapes had been entirely eliminated (swamp or custard-apple forest, peripheral wet prairie, and baldcypress stand), and other landscape types had been reduced by 74% (sawgrass plains), 47% (sawgrass-dominated mosaic), 24% (southern marl-forming marshes), and 13% (wet prairie/slough–tree island–sawgrass mosaic). On the local scale, wet prairie and slough decreased by 25%, and sawgrass marsh increased by 33%, a change attributed to lower water levels. Davis et al. (1994) discussed functional losses related to these changes: loss of total aquatic production due to reduction in spatial extent, loss of aquatic production in the southern Everglades due to shortened hydroperiod and interrupted flows, loss of habitat diversity at small scales, and reduction of dry-season feeding habitat of wading birds. Davis et al. (1994) concluded that the factors responsible for the historical configuration of habitats were extended hydroperiods and slow water flow caused by the presence of extensive sawgrass marshes, punctuated by drought years with severe fires.

The Everglades are facing additional threats: nonindigenous plant invasions and sea-level rise. Dominance of Australian melaleuca is estimated to be in the tens of thousands of hectares (Bodle et al. 1994; also see chapter on Nonindigenous Species), and sea-level rise is occurring at a rate 6 to 10 times higher than in the past 3,200 years, possibly affected by global warming (Light and Dineen 1994). Light and Dineen (1994) reviewed the role of agriculture in causing peat subsidence through increased oxidation of organic matter and suggested that the late 1900's may well have been the high point of agricultural production in the area because of the eventual loss of peat soils.

Pine Rockland and Tropical Hardwood Hammocks

Upland outcroppings of limestone in south Florida support pine rockland and tropical hardwood hammocks (Fig. 31) that are unique in the continental United States (Snyder et al. 1990). These ecosystems have been greatly reduced in extent by development and conversion to agriculture. Although wetlands have decreased by 40%–50% since 1900, the more restricted

Fig. 31. Peperomia vines and bromeliads show tropical growth forms on a live oak in a tropical hardwood hammock in Everglades National Park.

upland pine forests have decreased by 80% (Robertson and Frederick 1994). This loss of area brought with it increasing fragmentation—Robertson and Frederick (1994) estimated that distance between forest patches increased from 25 to 40 kilometers in the original landscape to 100–200 kilometers today. Not including Long Pine Key in Everglades National Park, only about 2% of the original pine rocklands persists, and only three of the extant tracts are more than 50 hectares (Snyder et al. 1990). The upland hardwood hammocks of peninsular Florida fared somewhat better; although many important and large stands were lost, about 50% of the original area is extant (Snyder et al. 1990). Most of the remaining stands of pine rockland and tropical hardwood hammocks in peninsular Florida are protected in Everglades National Park or by state or local governments. In contrast, most of the remaining undeveloped land in the Florida Keys is privately owned and likely to be developed (Snyder et al. 1990).

The upland forests of south Florida had higher rates of endemism of plants (42 plant taxa, including 12 species listed by Florida or the U.S. Fish and Wildlife Service as endangered or threatened) and animals (20–25 animal taxa, including 9 species listed by Florida or the U.S. Fish and Wildlife Service) than wetlands (no endemic plants and 2–3 species of vertebrates) (Snyder et al. 1990; Gunderson and Loftus 1993; Robertson and Frederick 1994). Further, the wetlands still retained their historical complement of vertebrates, although the uplands lost 26% of their breeding birds between 1920 and 1990 because of habitat fragmentation (Robertson and Frederick 1994). One plant species is presumed extinct from these habitats, three plant species have been extirpated, several color forms of the unique tree snails have been lost, and many of the endemic species are threatened (Snyder et al. 1990).

Even where upland vegetation is protected, species survival is not guaranteed. Fire is essential to the management of pine rockland vegetation, and pine and tropical hardwood hammocks are severely threatened by invasions of nonindigenous animal species (Snyder et al. 1990). Established nonindigenous animal species include 7 mammals, 30 birds, 4 amphibians, and 25 reptiles (Snyder et al. 1990). More research is needed before we know what effects these introductions are having on native species. Likewise, there are many plant invaders, several of which not only displace native species but also alter fire behavior and thus change the way the pine rockland ecosystem functions (Snyder et al. 1990).

The pine forests of the Florida Keys are lowlying and have limited supplies of fresh water. Ross et al. (1994) showed that pine coverage on Sugarloaf Key decreased from 88 to 30 hectares from 1935 to 1991, a loss they attributed to sea-level rise, documented at 15 centimeters over the last 70 years and thought to be accelerating now. Soil and groundwater salinity and the importance of salt-tolerant plants were higher where pines had died. Consequently, mangroves are likely to increase, and the landscape diversity of ecosystems and the number of terrestrial species will decrease in the coming decades (Ross et al. 1994).

Florida Scrub

A unique landscape of dense shrub thickets and taller pine forests occurs on the upland sands of the central ridge of the Florida peninsula (Myers 1990). The upland, or *high pine*, is related to the sandhills and longleaf pine flatwoods found broadly on the southeastern Coastal Plain. The scrub communities, dominated by oaks, rosemary, and pines, are more restricted to Florida and adjacent states, and those dominated by sand pine are restricted to Florida (Myers 1990). The distinctiveness of the scrub ecosystem is underscored by its high levels of endemism: scientists believe that 40%–60% of the species are endemic (Myers 1990).

Only scattered islands of these communities are extant. The Lake Wales ridge is an example of the biological importance of these remnants; it possesses the highest number of unique species, presumably because it has been above sea level for the longest period. This ridge contains a flora of which 30% is endemic, as well as the greatest concentration of federally listed species in eastern North America (Martin 1993). Federally listed plants number 13 and state-listed number 22 (Myers 1990). Sixteen plant species occur in 20 or fewer sites (Martin 1993). Five vertebrates are restricted to the Florida scrub, of which three are listed as threatened by the U.S. Fish and Wildlife Service (Florida scrub-jay, Florida sand skink, and bluetailed mole skink; Myers 1990).

Even though fire causes natural regeneration of scrub vegetation, this vegetation does not return to areas cleared for citrus (expanding southward in Florida because of recent freezes), homes, and businesses; in addition, scrub vegetation is greatly depleted when fire is excluded for long periods. As in all parts of Florida, the human population is rapidly growing in this region. Less than 10% of the natural scrub habitat is still found on the Lake Wales ridge, some in large tracts but much in small pieces scattered among housing developments and shopping centers. Although the trend is downward, several groups (U.S. Fish and Wildlife Service, The Nature Conservancy, Archbold

Biological Station) are working to protect the remaining scrub through acquisition and management (Martin 1993).

Mangroves

In the continental United States, well-developed mangrove forests occur only in south Florida (although mangrove species do occur in Louisiana) in areas where tidal waters produce saline conditions for all or part of the year (Fig. 32). Gilmore and Snedaker (1993) described four types of mangrove communities determined by the salinity regime, which, in turn, is determined by topography and surficial hydrology. Mangroves exist in a tension zone between saltwater flows and freshwater flows from inland areas; in addition, these forests are frequently battered by tropical storms, resulting in an ecosystem often dominated by patches of trees with different age classes.

There are about 202,000 hectares of mangrove forests in Florida (Gilmore and Snedaker 1993). Odum and McIvor (1990) reviewed data that indicated a loss of about 2.5% of the mangrove habitat between 1943 and 1970 in the three counties with the highest original total. They noted, though, that the rate of loss was quite uneven from place to place; for example, in Tampa Bay, 92% of the mangrove forest habitat was lost to impoundment between 1955 and 1974, and 44% of the estuarine areas have been lost (Gilmore and Snedaker 1993). Overall areal extent of this habitat has been reduced by development (draining and filling for urban areas and mosquito control), by reductions in freshwater flow because of diversion of runoff from inland areas (these reductions change salinity and alter productivity within the mangrove forests), and by invasion of nonindigenous species. Coastal mangrove forests dominated by red mangrove were protected by Florida law starting in the 1970's, but Gilmore and Snedaker (1993) reported continuing losses due to poor enforcement and disregard of this protection, as well as to legal but detrimental pruning of mangrove trees. Moreover, mangrove forests that are more inland have no protection on private land and thus are currently dependent on public lands for their survival. The large stands on public lands in the Everglades National Park have been affected in unknown ways by past reductions in freshwater flows and by other human influences (Gilmore and Snedaker 1993). In the future, sea-level rise (10–15 centimeters per century and probably accelerating) may increase the area dominated by mangroves in areas with a low topographic gradient (Odum and McIvor 1990).

Although plant species richness is not high in these ecosystems, the habitat is highly productive and diverse in other groups. Gilmore and Snedaker (1993) listed seven guilds of animals determined by spatial position. Mangrove forests are extensively used by larval and juvenile fishes and invertebrates and probably play critical roles in the survival of many species of tunicates, crustaceans, mollusks, insects, and fishes. Mangrove forests provide habitat for species that are important in regional fisheries, as well as for eight species that are listed as threatened or endangered by the U.S. Fish and Wildlife Service (Odum and McIvor 1990).

Fig. 32. Mangrove forests dominate the dynamic coastlines of southern and central Florida.

Aquatic Ecosystems

Freshwater habitats in the Southeast include standing and flowing waters (Fig. 33). Rivers and streams range from the fast and clear high-elevation streams of the southern Appalachians to the slow and often opaque rivers of the Coastal Plain (Adams and Hackney 1992). In areas of karst topography, *lost* or *disappearing streams* are aboveground only during high water, and underground drainage in cave systems is important. Although few large lakes occur naturally in the Southeast, there are thousands of small ponds (Crisman 1992). In addition, many lentic ecosystems (ponds, reservoirs, and impoundments) were made by humans.

Rivers and Streams

Isphording and Fitzpatrick (1992) described the Southeast's rivers and streams as an evolutionary laboratory. There are 30 major river systems that drain to the Gulf of Mexico or the Atlantic Ocean. Long isolation of these waters has produced high species richness and local endemism. Continental high points in diversity occur in fishes (535 species), salamanders (51 species in 19 genera), aquatic insects

Courtesy, N. Burkhead, USGS

Fig. 33. Virginia's Roanoke River is home to an endangered fish, the Roanoke logperch.

(Wallace et al. [1992] suggested that undescribed species equal described species in some groups), crayfishes (300 species in 11 genera), and many mollusks (for example, mussels with 270 species and subspecies in 49 genera [Isphording and Fitzpatrick 1992], and freshwater snails with 118 species in 9 families in the Mobile River basin [Bogan et al. 1995]). Taxonomic revision is ongoing in these groups, and new species are still being discovered. Systematic and genetic relatedness among the species has been used to describe biogeographic provinces and evolutionary histories (for example, Sheldon 1988). Six broad geographical provinces were based on several animal groups (fishes, mollusks, and crayfishes): the Atlantic Coastal Plain, the eastern Gulf Coastal Plain, the southern Appalachians, peninsular Florida, the Great River (Ohio–Mississippi) systems, and the trans-Mississippi region (Isphording and Fitzpatrick 1992). The faunas of the Atlantic Coastal Plain and the eastern Gulf Coastal Plain had their origins in different parts of the southern highlands. The southern Appalachians have a high degree of endemism in isolated headwater streams.

Southeastern stream systems have been altered by human activities, including impoundment, channelization, lowering of water tables, increased runoff, acid mine drainage, air and water pollution, sedimentation, recreation, and introduced species (including mussels, fishes, and aquatic plants). Many examples of effects on stream biota can be cited (Hackney et al. 1992)—nearly all major stream systems have been channelized or dammed (Adams and Hackney 1992). In the Southeast, 144 major reservoirs have been built (Soballe et al. 1992), and one-third of all Florida rivers have impoundments. The closing of the Norris Dam on the Clinch River in Tennessee in 1936 caused a loss of 45 mussel species below the dam within 4 months (Soballe et al. 1992). The creation of the Tennessee–Tombigbee Canal is allowing mixing of formerly isolated native biota; Sheldon (1988) predicted this mixing will result in species loss through competition and interspecific hybridization. Between 1930 and 1971, 2,017 square kilometers were surface-mined in the Appalachian Highlands, leading to acidification of nearby streams and reductions in aquatic species diversity and biomass (Mulholland and Lenat 1992). Water hyacinth, a nonindigenous plant first introduced to New Orleans in 1884, had become a problem locally by 1890 and covered 80,000 hectares in Florida by 1975 (Crisman 1992).

Only 20% of the nation's freshwater communities are protected by federal laws, and of these, only 10% are east of the Mississippi (Benke 1990). Despite having the highest diversity of fish species in the United States (McAllister et al. 1986), the rivers and streams of the Southeast are little understood and only minimally protected. Lotic species (those that live in moving water), especially those of higher elevations, are most seriously affected, as their specialization to clear, fast-moving streams renders them unable to adapt to conditions caused by dredging or impoundment (Hackney and Adams 1992).

Caves

The Southeast has about two-thirds of all U.S. caves that are more than 3 kilometers long, one-half of the 49 deepest U.S. caves, and a total of some 20,000 individual caves, including Mammoth Cave in Kentucky, the world's largest cave system (Hobbs 1992). These caves are distributed over several physiographic provinces but are most abundant in the Interior Low Plateaus of Kentucky and Tennessee, the Ozarks, and the Coastal Plain of Florida and adjacent Georgia. Springs, including thermal springs in Arkansas, Georgia, Maryland, North Carolina, Virginia, and West Virginia, are often associated with areas where cave systems are common.

The caves and springs of the Southeast have a diversity of unique organisms, including 10 federally listed endangered species and 140 state-listed species (Hobbs 1992). All 6 species of the cavefish family are largely confined to the Southeast. Many of the larger species, such as blind fishes and salamanders, are vulnerable to extinction because of narrow physiological tolerances, long-delayed reproduction, and low reproductive outputs, traits that may have been selected because of their historically stable cave environments.

Although 62 cave complexes are protected (Hobbs 1992), survival of cave ecosystems depends on successful management of terrestrial systems and water quality. Caves depend on outside sources of detritus (plant material) for energy flow and are threatened by changes in the quantity and quality of water flowing from terrestrial sources. The late 1980's organization of an International Biosphere Reserve around Mammoth Cave National Park seeks to develop cooperative management of water resources among public and private partners to protect that cave system.

Natural Lakes and Ponds

Natural lakes and ponds in the Southeast are mostly small and were formed because of special characteristics of landform and geology. The two most common lake types are the Carolina bays and Florida solution ponds on carbonate bedrock (Crisman 1992). In addition to numerous ponds in Florida, solution of carbonate bedrock has produced sagponds in the southern Appalachians and the limestone sinkhole ponds of the Interior Low Plateaus (Crisman 1992).

In addition to Carolina bays and solution ponds, there are five other lake types in the Southeast (Crisman 1992): oxbow ponds and other ponds formed by the dynamics of erosion and deposition in river valleys, coastal ponds formed when streams are blocked by dunes and longshore deposition of sands or when basins are created by storm surge (most common in the Florida Panhandle), lakes formed by landslide blockage of mountain streams (for example, Mountain Lake in Virginia), lakes formed by local subsidence of the land surface (for example, Reelfoot Lake in Tennessee), and lakes formed by uplift of marine basins (for example, Lake Okeechobee in Florida). Most lakes and ponds are small, although the large lakes include Lake Okeechobee in Florida, the second-largest lake wholly within the United States, and Reelfoot Lake in Tennessee, formed by the New Madrid earthquake in 1811 (Crisman 1992).

Beavers were historically important in creating ponds on stream basins in the Southeast. Although the native subspecies of this animal became extinct in the Southeast by about 1900, recently a northern subspecies of beaver has spread through the Southeast after several releases by game managers between 1930 and 1950. The beaver was important in the natural dynamics of rivers and in maintaining habitat diversity. In some areas now, however, this species is entering a predator-free and fragmented landscape and may be threatening remnant natural areas.

Principal threats to natural ponds and lakes include eutrophication, acidification, drainage, control of water-level fluctuation, and invasions by nonindigenous species. Crisman (1992) noted that a serious hindrance to documenting these effects is the lack of an understanding of the composition, dynamics, and natural variation in these systems.

Status and Trends of Fishes, Freshwater Mussels, and Macroinvertebrates

Freshwater Fishes

The Southeast has 535 native freshwater fishes in 31 families (Lee et al. 1980; Echternacht and Harris 1993; Fig. 34; Table 11), making this region the richest of any temperate area of comparable size in the world. The total number of species represents 65% of the freshwater fishes of the United States, with 48% (257 species) of the southeastern species found nowhere else in the country. Fifty additional species are marine fishes that occasionally invade fresh water. Ten additional species live in the sea but spawn in fresh water, and one species, the American eel, lives in fresh water but spawns in the sea. Thirty-five nonindigenous species have become established in this region. Diversity is also high at smaller sampling scales. Cells of one-degree latitude and longitude typically have 25–50 species, and some have as many as 73. Elsewhere in North America the number at this scale is typically 5 to 15 (McAllister et al. 1986).

The high species richness is the result of diverse aquatic habitats and historical factors

Courtesy N. Burkhead, USGS

Fig. 34. A Gulf sturgeon, a threatened species, swims in a spring on the Suwannee River. Sturgeons, which are one of the oldest existing fish species, were once common on Gulf of Mexico rivers, which these fish ascended in the spring to spawn. Dams and pollution have severely reduced Gulf sturgeon populations.

that have permitted longer periods of isolation with sporadic interbasin dispersal (Sheldon 1988). Sea-level change during the Ice Age affected the distance between the mouths of rivers, which provided alternating periods of isolation and opportunities for dispersal. Stream capture in the highlands also allowed rare but significant opportunities for interbasin dispersal. Geographical differentiation in fishes has been used to define seven faunal regions: southern Appalachians, Interior Plateau, Lower Mississippi River, Lower Mobile River basin, Atlantic Slope, Lower Appalachicola River basin, and peninsular Florida (Walsh et al. 1995; Table 12).

Sheldon (1988) demonstrated that there is a strong species–area relationship for freshwater fishes but that, in a given basin area, the isolated rivers that flow directly to the Atlantic Ocean or Gulf of Mexico had fewer fish species than comparable river segments (similar basin area and habitat diversity) within larger, more-branching river systems (for example, the Mississippi and its large tributaries). Sheldon also showed the importance of separate evolution in isolated drainage basins in increasing the number of regional species. He predicted from species–area relationship that the Tennessee–Tombigbee Canal, which links two long-isolated and species-rich basins, will eventually result in a decline in the number of species—the connected system will not be able to support as many species as the two systems could support when isolated.

Human-caused changes to rivers and streams have greatly imperiled the Southeast's rich fish fauna (Johnson 1995; Williams and Neves 1995). About 19% of the region's species are endangered or threatened, and this percentage has increased through time (Johnson 1995). At present, there are 30 fish species listed by the U.S. Fish and Wildlife Service, 23 of which are narrowly restricted endemics. The high percentage of imperiled species in the southern Appalachians (Table 12) reflects the presence of narrowly restricted endemics (Fig. 35) in headwater streams, the dependence of many species in that region on good water quality in small rivers and streams, and the vulnerability of such streams to disturbances in their watersheds. The high percentage of imperiled species in the Interior Plateau region reflects the presence of species endemic to cave systems (Fig. 35).

There are many examples of fragmentation of the range of fishes and the extirpation of others from entire river systems. The loss of individual populations is probably the most significant change now occurring but is not well documented until a species is on the verge of extinction. Three species have become extinct: Maryland darter, harelip sucker, and whiteline topminnow (Miller et al. 1989; Walsh et al. 1995). The least darter has been extirpated in the Southeast but populations persist elsewhere, and only a few individuals of the slender chub have been seen since the mid-1980's (Walsh et al. 1995; Fig. 36).

Narrowly restricted endemics, short-lived species, and species dependent on good water quality are particularly vulnerable. Nearly all of the 30 species that are federally listed are narrowly restricted endemics with limited tolerance for habitat modification. The extinct whiteline topminnow is an example of a narrowly restricted endemic; it was found only in a single Alabama spring that was used to supply

Table 11. Federally listed vertebrates. The numbers of native, endemic, extinct, and extirpated species are taken from Echternacht and Harris (1993). The numbers of narrowly restricted endemics (species limited to only one or a few states and a narrow habitat breadth) and listed species are from U.S. Fish and Wildlife Service (1994).

Group	Number of species listed as					
	Native	Endemic	Extinct	Extirpated	Narrowly restricted endemics	Listed endemics
Fishes	535	257	3	2	30	23
Reptiles and amphibians	242	83	0	0	12	8
Birds	237	0	2	3	13	4
Mammals	101	7	0	5	22	13

Table 12. Imperiled fish species as a percentage of the total number of species by faunal region (from Walsh et al. 1995).

Faunal region	Percent of species endangered or threatened
Southern Appalachians	18.3
Interior Plateau	11.4
Atlantic Slope	7.1
Lower Appalachicola River basin	6.3
Lower Mississippi River	6.0
Lower Mobile River basin	4.9
Peninsular Florida	4.1

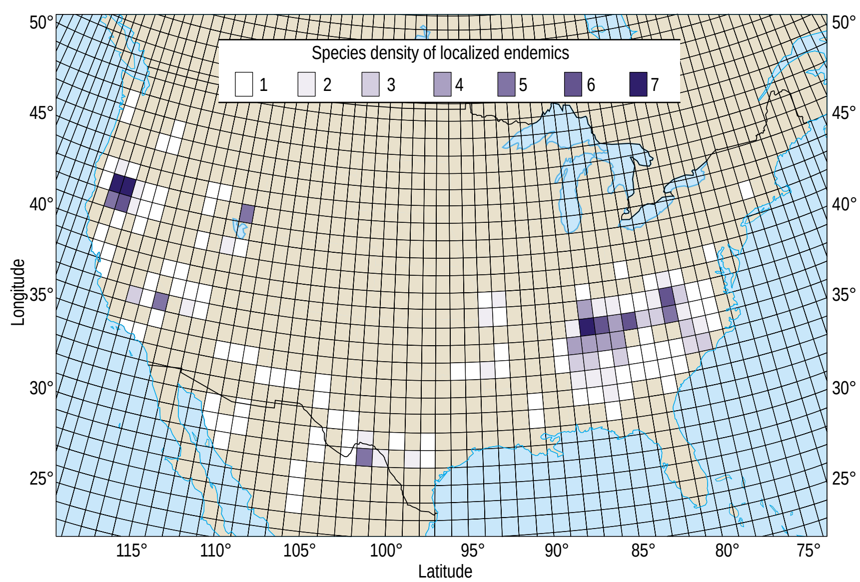

Fig. 35. Distribution of endemic fish species in the Southeast, as compared with the rest of the contiguous U.S., on a grid of one-degree latitude by one-degree longitude (redrawn from McAllister et al. 1986).


Courtesy N. Burkhead, USGS

Fig. 36. Only a few individuals of the threatened slender chub have been observed since the mid-1980's despite intensive surveys by scientists. More effort is needed to determine if this small minnow is still extant.

water for the city of Huntsville. The Waccamaw silverside, confined to a single Coastal Plain lake in North Carolina, is vulnerable because of its narrow range and short-lived nature (it is an annual species). Other endangered species are not so restricted, however; for example, the harelip sucker was found in eight states. This species, last collected in 1893 but probably persisting to the early 1900's, appears to have been restricted to clear-water pools with rocky substrates in moderate to large streams, a habitat vulnerable to siltation and agricultural runoff (Miller et al. 1989).

A recent assessment of the habitats of threatened fish species in Tennessee found that medium-sized rivers were especially important (Etnier and Starnes 1991). Only 14% of all fishes reported in Tennessee occur in medium-sized rivers, but 41% of the fish species on the state's threatened and endangered species list depend on the habitat medium-sized rivers provide. These fishes are threatened because of impoundments already constructed or pending and because they are sensitive to the loss of coarse substrates caused by sedimentation. However, the imperiled species were distributed across a variety of habitats: large creeks and small rivers (21% of threatened species), streams (16%), springs (13%), and big rivers (9%).

Many investigators have suggested the need for long-term monitoring to detect trends and natural fluctuations in fish populations. Bass (1990) reported that fish trends in Florida from 1983 to 1987 revealed some flux of species in individual rivers during this period but no statewide decline. Bass (1990) concluded that monitoring is critical to understanding natural fluctuations and to detecting long-term trends.

Freshwater Mussels

The Southeast's freshwater mussels include 270 species and subspecies in 49 genera, representing 90% of the freshwater mussel fauna of all of North America north of Mexico (Williams et al. 1993). Ten genera are endemic to the Southeast. Of 93 species and subspecies limited in the United States to one or two states, 91 occur only in the Southeast. The species richness of freshwater mussels in the Southeast is attributed to habitat diversity (including substrates of attachment), evolution within isolated river basins, stream capture over geologic time (which produces new patterns of dispersal and isolation), and high richness in fish species (larval forms use fish as hosts).

Forty-eight percent of the freshwater mussels of the Southeast are endangered, threatened, or possibly extinct (Williams et al. 1993; Williams and Neves 1995). An additional 25% are of special concern, resulting in 73% of this diverse fauna being at risk. Only 25% of the fauna is considered stable (Williams et al. 1993). Of 21 species that are now potentially extinct, 14 were endemic to the Southeast (Williams et al. 1993). Declines in freshwater snails and other mollusk groups are probably also occurring in the Southeast, but surveys of these groups are less complete.

Declines in mussel faunas have affected river basins regionwide, including those with higher and lower amounts of endemism. Historically, diversity of mussels increased from headwaters to the mouths of rivers; pollution and other human influences also increase in this direction. Hence, declines in diversity have been most significant in the lower reaches of rivers. Habitat specialists (those requiring, for example, a particular kind of hard substrate) have declined more than habitat generalists.

Factors that are important in declines in mussel richness and abundance are sedimentation, pollution, changes in river flow due to dams and channelization, invasions of nonindigenous species (for example, the zebra mussel and Asian clam), and loss of fish hosts. In addition, commercial harvest of mussels is causing unknown effects on target and nontarget species (Williams et al. 1993). As with other aspects of aquatic diversity, retention of natural vegetation in floodplains and along riverbanks is a key element in the protection of water quality and mussel populations. Many southeastern states still have areas with high mussel diversity and abundance, such as the Clinch River in Virginia, Swift Creek in North Carolina, Stephens Creek in South Carolina, and the Ogeechee River in Georgia. These waters tend to be tributary and headwater rivers within drainage basins of several hundred square kilometers in which silviculture is the dominant land use and agricultural and urban areas are limited.

No regionwide monitoring or conservation plan exists for freshwater mussels. Conservation efforts will require cooperation of many public and private groups because mussel populations ultimately depend on water quality that is affected by human activities over large areas. The growing human population and its need for sources of clean drinking water will increase the pressure for the creation of additional reservoirs, which in turn will further imperil this distinctive element of the southeastern fauna.

Benthic Macroinvertebrates and Water-Quality Trends

The Clean Water Act directs the U.S. Environmental Protection Agency to evaluate, restore, and maintain the chemical, physical, and biological integrity of our nation's waters. In response, state environmental protection agencies have implemented water-quality monitoring programs that are chemically based and that have successfully addressed water-quality issues (U.S. Environmental Protection Agency 1990). Chemical monitoring alone is not adequate for describing water-quality changes, however. Spills and rapid fluctuations in effluent characteristics can go undetected in routine monitoring of water chemistry. Pollution from nonpoint sources can arrive with rain and runoff between routine sampling dates. To address these concerns, most state programs have supplemented chemical monitoring programs with biological monitoring programs, which often include the assessment of benthic macroinvertebrate (aquatic insect larvae) populations but may also include fish, periphyton, and phytoplankton populations. All but four states conduct some form of biological water-quality monitoring (U.S. Environmental Protection Agency 1991). Used together, chemical and biological water-quality monitoring programs provide a comprehensive, integrated approach to water-quality assessment.

Benthic macroinvertebrates are sensitive to subtle changes in water quality. Because many species have life cycles of 6 months to 1 year, the effects of a short-term pollutant (such as a spill) will not be overcome until the next generation appears (Lenat 1993; Patrick and Palavage 1994). Benthic macroinvertebrate communities have also been shown to respond differently to different water-quality problems. Typical responses include declines in richness and increases in abundance of tolerant taxa as a response to nutrient enrichment, decreases in richness and abundance in response to toxic effluents, and stability in richness and declines in abundance in response to sedimentation (Lenat 1993; Patrick and Palavage 1994).

Biological surveys typically fall into two primary categories: network trend monitoring and intensive surveys at selected locations to assess effects from specific sources. In trend monitoring, biological data are collected from fixed stations over set intervals. For example, in North Carolina before 1990, the Division of Environmental Management maintained a Benthic Macroinvertebrate Ambient Network by using stations of the ambient water-quality monitoring program. North Carolina and many other states have been conducting monitoring programs organized around river basins (Fig. 37). In this system, sampling is concentrated in one large river basin or in as many as six smaller ones each year so that all river basins are eventually surveyed during a 5-year period. The basinwide program uses many of the original stations of the ambient water-quality program.

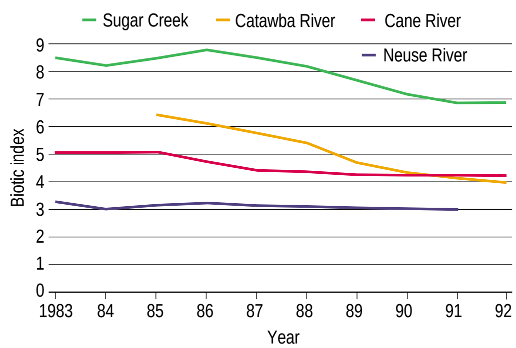

Fig. 37. Trends in water quality for four North Carolina river systems, as indicated by benthic macroinvertebrate monitoring. The North Carolina Biotic Index (Lenat 1993) is a summary measure of the tolerance values of specific macroinvertebrates relative to their abundance; the index serves as a measure of the general level of pollution regardless of source or stream size. A high biotic index indicates poor water quality. In this figure, Sugar Creek, in the Piedmont of South Carolina, and the Catawba River, near Mt. Mitchell in western North Carolina, both show improvement in water quality over the past decade. The Cane River, north of Mt. Mitchell, and the Neuse River, southeast of Raleigh in the Piedmont, North Carolina, have shown little change in water quality (D. Penrose, North Carolina Department of Environment, Health, and Natural Resources, unpublished information).

Although most states have collected biological data for fewer than 10 years, nonetheless, evaluation of water-quality trends has been possible. In North Carolina, improvements in biological communities have been detected as a response to a phosphate ban and upgrades to wastewater treatment plants. Macroinvertebrate communities also improved after an upgrade to a pulp and paper mill that was polluting a section of the Pigeon River, a problem that resulted in the state of Tennessee suing the state of North Carolina.

Patrick and Palavage (1994) argued that surface waters have improved the most where they have had the greatest degree of regulation. Unregulated sources, such as runoff from agricultural and urban areas, appear to play the major role in stream degradation in the Southeast (Duda et al. 1979; Benke et al. 1981; Lenat and Crawford 1994). Agricultural activities result in greater concentrations of most dissolved substances, greater levels of sedimentation, and higher concentrations of nutrients (Lenat and Crawford 1994). Urban runoff, on the other hand, can be a mixture of different pollutants, including enrichments, sediments, and toxic metals.

The scarcity of long-term biological data from streams and rivers has sparked interest in monitoring; most state and federal agencies have programs to address biological integrity. Federal programs include the U.S. Geological Survey's National Water Quality Assessment Program, a nationwide program designed to assess the status and trends in the quality of surface-water and groundwater resources of entire river basins (Gurtz 1993). Ten of the 60 river basins included in this program are in the Southeast. If this project continues, it will provide a much-needed basis for the future assessment of aquatic trends in the country.

Status and Trends of Reptiles, Amphibians, Birds, and Mammals

Reptiles and Amphibians

Reptiles and amphibians are present in virtually all natural habitats in the Southeast. All the turtle species nest on land, some aquatic turtles and snakes hibernate on land, and dozens of species of southeastern frogs and salamanders are terrestrial as adults but require wetlands for breeding and development of young. Also, terrestrial corridors among aquatic habitats are essential for reptile and amphibian dispersal during unfavorable periods such as drought.

Of the more than 450 species of reptiles and amphibians native to North America, more than half (242 species) occur in the Southeast (Conant and Collins 1991; Echternacht and Harris 1993; Gibbons 1993; Table 11). The Gulf Coastal Plain is the most significant area of endemism in reptiles and amphibians in the United States (Dodd 1995a)—40% of southeastern amphibians and 29% of southeastern reptiles are endemics. In addition, there are 4 species of introduced amphibians and 20 species of introduced reptiles in the Southeast, most of which are found in the Coastal Plain and Florida.


Courtesy of Savanna River Ecology Lab

Fig. 38. The Appalachian salamander, an endemic species of the southern Appalachians.

The Southeast has the highest regional total (130 species) of amphibians in the United States (Echternacht and Harris 1993), including 38 species of frogs and toads (12 of these are endemic to the Southeast) and 92 species of salamanders (45 of which are endemic to the Southeast; Fig. 38). The southern Appalachians are a world center of diversity for salamanders and have 68 species of a unique group of lungless salamanders that evolved in this region of well-oxygenated streams and high rainfall. The Southeast has 6 species of large, fully aquatic salamanders and the Coastal Plain has 32 species of frogs and toads, of which 11 are endemic.

There are 52 species of snakes in the Southeast, of which 11 are endemic (Conant and Collins 1991; Echternacht and Harris 1993). Of the 91 species of lizards native to the United States (the only group of U.S. herpetofauna concentrated more heavily in another geographic region—the Southwest [Stebbins 1966]), 21 occur in the Southeast, and 6 of these are endemic. The Southeast has 36 species of turtles, 13 of which are endemic; the Coastal Plain possesses North America's highest diversity in this group. One of the two greatest concentrations of freshwater turtle species in the world (the other is in Asia) is in the Mobile River basin (Iverson 1992; Lydeard and Mayden 1995).

The only crocodilians in the United States, the American alligator and American crocodile, are restricted to the Southeast. From northeastern North Carolina southward, the American alligator is recovering from past population declines (Stalter and Odum 1993; Woodward and Moore 1995). Woodward and Moore (1995) estimated increases in Florida populations of 1.9% per year since the mid-1970's and concluded that reproduction is probably sufficient to balance the recent revival of legal hunting. The ecological role of the American alligator is highly significant: the reptile creates pools in the marshes that serve as habitat for many other species.

Although there have been no documented extinctions in these groups, 12 species are listed as endangered or threatened by the U.S. Fish and Wildlife Service: American alligator, American crocodile, blue-tail mole skink, Florida sand skink, Eastern indigo snake, gopher tortoise, 4 turtle species, and 2 salamander species. All of these except one mountain salamander species occur on the Coastal Plain. Eight of the 12 species—the 4 turtles, 2 skinks, and 2 salamanders—are narrowly restricted endemics. The gopher tortoise has become threatened in part because of the loss of longleaf pine habitat (Bury and Germano 1994). The American alligator is a wide-ranging animal that was formerly reduced by hunting and human alteration of aquatic habitats and now has recovered so that hunting has been reinstituted in some areas (Woodward and Moore 1995).

The greatest threat to reptiles and amphibians comes from habitat loss and changes in water quality. Numerous examples can be given of population declines in individual wetlands as a consequence of human activities. Drainage and destruction of temporary ponds have resulted in the reduction of striped newts in Georgia (Dodd 1995a), the extirpation of the flatwoods salamander from a portion of its range, and apparent declines of gopher frogs in Alabama and Mississippi (Dodd 1995a).

Species that are adapted to terrestrial habitats have also suffered. Of the 242 native reptiles and amphibians in the Southeast, 170 (74 amphibians, 96 reptiles) are native to longleaf pine–wire-grass ecosystems (Dodd 1995a). The near loss of this natural community, through timbering, development, and fire suppression, has had a significant, though largely unquantified, effect on reptiles and amphibians.

Several species of map turtles, which are native to large southern rivers, have presumably been severely affected by impoundments. The ecological status of some of these turtles has also been affected by the removal of dead trees and the dredging of river bottoms, which harbor mollusks that the turtles eat. The opportunity has passed for us to measure the effect on historical population levels, even within the last century, but most scientists agree that many populations of map turtles are declining (Buhlmann and Gibbons 1996).

Some musk turtles are restricted to stream systems; the flattened musk turtle from Alabama, for example, represents a species whose very existence has been jeopardized by water-quality degradation. The negative effects have been not only from direct health effects on these turtles but also from the elimination of their basic food supply, the freshwater mollusks that live in the streams (Lydeard and Mayden 1995; Buhlmann and Gibbons 1996).

Spotted turtles (Fig. 39) are a clear example of how humans can cause a reduction in a species' population sizes and numbers. Destruction of small wetlands is one obvious assault on this species; spotted turtles have special habitat requirements and do not persist in other aquatic habitats, such as farm ponds, once their wetland homes are destroyed. In addition, the spotted turtle is threatened because of legal collection by commercial collectors (for example, more than 500 turtles were collected in North Carolina in 1993; A. Braswell, North Carolina State Museum, Raleigh, personal communication). For a species that lives in small, isolated wetlands, usually in low numbers, removal of several adults from a habitat can be devastating to a population (Congdon et al. 1993).

Commercial collecting for the restaurant trade has also had an effect on some reptile populations. For example, the alligator snapping turtle and the common snapping turtle are severely and negatively affected by commercial enterprises that remove many individuals of these long-lived species.

It is critical to realize that in one major respect, most reptiles and amphibians are not like game species such as deer or northern bobwhite—their populations are not sustainable if adults are removed. Individuals of most reptile and amphibian species take years, often more than a decade, to reach maturity. Populations are often disjunct and the numbers of individuals small. Such species are sensitive to abrupt reductions in population size and cannot replace themselves when subjected to harvest (Congdon et al. 1993).

Courtesy of Savanna River Ecology Lab

Fig. 39. A spotted turtle, which is one of the Southeast's 36 species of turtles and one whose numbers are declining.

Highway deaths also deplete the numbers of many species of reptiles and amphibians that travel overland. A 2-meters-long indigo snake, for example, does not move fast enough to safely get across today's highways.

Some ecologists have reported declines in amphibian populations and related these to specific threats, such as acid rain, destruction of the ozone layer, global warming, or other forms of nonpoint pollution (Blaustein 1994). It is unclear if any of these factors are responsible for amphibian declines in some regions (Pechmann et al. 1991; Pechmann and Wilbur 1994), but habitat destruction is the primary threat to most species of reptiles and amphibians in this country and probably in most countries in the world today. Timber harvest, for example, dramatically reduces amphibian populations in the southern Appalachians (Petranka et al. 1993). Habitat destruction may take more subtle forms, though, and what may appear to be protected and pristine habitat may actually be experiencing degradation because of changes in hydrology, pollution, herbicide and pesticide runoff, the introduction of competitive nonindigenous species, the introduction of disease organisms, or the loss of important breeding sites such as temporary ponds (Blaustein 1994; Dodd 1995b).

No modern extinction of a reptile or amphibian species has yet occurred in the Southeast, but there are many examples of long-term declines in the numbers of individuals and populations. Amphibian declines are difficult to assess because of natural population fluctuations; more long-term information is needed to better interpret trends in amphibian populations and to discern natural and anthropogenic causes (Pechmann et al. 1991; Blaustein 1994; Pechmann and Wilbur 1994).

Insufficient knowledge of the distribution and ecology of native reptiles and amphibians is a major shortcoming in any national effort to detect change and avoid loss in this group. An example of the difficulty that ecologists face in confirming the presence of herpetofauna is apparent from studies by investigators at the Savannah River Ecology Laboratory and from studies by other investigators on the Savannah River Site in South Carolina. This site is the largest tract of land (750 square kilometers) in North America with high herpetofaunal species diversity and a long-term record of intensive ecological research and survey. Since the 1950's, herpetologists have collected data on more than a million individual reptile and amphibian specimens representing more than 100 species (Gibbons and Semlitsch 1991). Nonetheless, despite intensive surveys, the presence of new species has been verified on the Savannah River Site at a rate of more than five species per decade.

Birds

The Southeast originally had 237 native species of birds, none of which were strictly endemic to the region (Echternacht and Harris 1993; Table 11). Three species are nearly restricted to the Southeast: Bachman's warbler (which may be the rarest vertebrate in the region), Swainson's warbler, and the brown-headed nuthatch. Twenty-six percent of the total (61 species) is associated with water. Of these, 19 are large wading bird species, a group for which the Southeast has the continent's highest total. The greatest species richness of birds occurs in the coastal wetlands. Thirty-one species (13.4%) are restricted to the high mountains. Echternacht and Harris (1993) estimated that there are 17 established nonindigenous bird species in the Southeast, but they warned that the number may be an underestimate, considering that other species have been released in the area.

Land clearing and hunting were responsible for the extinction of two bird species in the Southeast: the passenger pigeon (last reported in the wild in 1899) and the Carolina parakeet (last reported in the wild in 1913). Passenger pigeons were hunted for their market value whereas Carolina parakeets, birds of old wetland forests, were hunted to protect fruit crops.

Three species have been extirpated from the Southeast: ivory-billed woodpecker (last seen in the 1950's and thought to persist in Cuba), which was dependent on large-cavity trees in extensive and old riparian forests; and the Zenaida dove and the Key West quail-dove, which were rare Caribbean species restricted to Florida— the reason for their extirpation is not known (Echternacht and Harris 1993). An additional subspecies, the dusky seaside sparrow, became extinct because of poor fire management of its marsh habitat in coastal northern Florida.

Fourteen species and subspecies of birds are federally listed, of which 12 are Coastal Plain species: crested caracara, Mississippi sandhill crane, Florida scrub-jay, brown pelican, piping plover, Cape Sable seaside sparrow, dusky seaside sparrow (now extinct), wood stork, least tern, Bachman's warbler, ivory-billed woodpecker, and red-cockaded woodpecker. The fate of these species is largely tied to habitat loss, including reductions in longleaf pine savannah, Florida scrub, wetlands, and beach communities. Two other federally listed species, the bald eagle and the peregrine falcon, were formerly wide-ranging species sensitive to pesticides; these species are now recovering.

The Southeast is important not only for summer breeding populations but also for birds that winter in the Southeast and for birds that migrate farther distances (for example, to the Caribbean and Central and South America) after passing through the South in spring and fall. Coastal habitats, maritime forests, and longleaf pine savannah are all important to migrating species. Threats to bird species include land-use changes, forest fragmentation (which often results in increased nest predation and cowbird parasitism), tropical deforestation (for Neotropical migrants), elimination of wetlands, and coastal development.

Several investigators have published summaries of trend data for bird species in the United States. By using the Breeding Bird Survey data for 1966 to 1992, Peterjohn et al. (1995) reported that birds of grassland and shrubland experienced the most significant and consistent declines; fully 82% of grassland species declined over this period. General results indicate that there were declines in specialist species and those that depend on natural habitats, whereas there were increases in generalist species that adapted well to use of agricultural landscapes.

Hunter (draft report) used the same data base to support this conclusion for the Southeast: of 14 bird species that occur in grassland habitats (including coastal prairies in Texas and Louisiana and longleaf pine savannahs), 8 significantly declined, and only 1 significantly increased. Average population declines per year varied from 1% to 6% (vesper sparrow). These habitats harbor 10 endangered bird species and 5 candidate species. Hunter also showed that of 24 bird species in successional shrub–scrub vegetation, 14 species experienced significant population declines ranging from 1% to 5.8% per year. The eastern Bewick's wren (5.8% per year) and the golden-winged warbler (5.4%) experienced the greatest declines.

Root and McDaniel (1995) studied trends in 27 species of songbirds by using the Christmas Bird Count data from 1959 to 1989. They found that in the United States, the largest decreases of these species were in the Southeast. On a per state basis, 10%–30% of the 27 species were declining in southeastern states, whereas, with the exception of South Carolina (25% of the birds increasing), 0% to 5% of the species showed increases. They also found that birds of open habitats that depended on the seeds of grasses and herbaceous plants (for example, sparrows and meadowlarks) experienced the greatest declines.

In these data sets, about half of the Neotropical migrants showed increases and half decreases (Peterjohn et al. 1995). Declines of about 1%–2% per year have also been observed in area-sensitive woodland birds such as the wood thrush and veery (Peterjohn et al. 1995; Root and McDaniel 1995). The loggerhead shrike declined by 3.2% per year (Yosef et al. 1993; Peterjohn et al. 1995).

Some bird species, though, have increased in the last several decades, pointing to significant conservation success stories. For example, the brown pelican population has increased by 3.8% each year, at least in part because of the banning of DDT (Erwin 1995). Several species of raptors have also increased because of the banning of DDT, protection, and habitat management (Fuller et al. 1995). The endangered Mississippi sandhill crane, originally found from Alabama to Louisiana but now known from only one site in Mississippi, has increased because of intensive conservation management (Gee and Hereford 1995; Peterjohn et al. 1995). That species reached a low point of 13 individuals in the wild in 1985; there are now 20 individuals in the wild, with an additional 115 birds released from captive breeding (Gee and Hereford 1995). Egret populations were drastically reduced in the early 1900's because of hunting for the plume trade; populations are recovering and have increased by an average of 2% per year (Erwin 1995).

Critical information for the conservation of bird species includes understanding the relationship between reproductive success and habitat size and quality. Hunter (draft report) stated that to create populations that will endure and that will generate excess individuals to colonize new sites, some birds species (for example, the ivory-billed woodpecker) require 2,000 to 40,000 hectares of unbroken habitat. Further, we have to understand the relation between reproductive success and such microhabitat variables as forest-age structure. Hunter also reported that species that require large areas can act as umbrella species for species with smaller area requirements. If we understand the habitat area each bird species needs, it will help us determine optimum block sizes and rotations for harvested forests. The need for large habitat areas is another argument for reforestation of marginal farmlands and the retention of wetlands. Because the southeastern landscape is so heavily in private ownership, land used for agriculture and forestry must play a large role in the survival of bird species diversity. Erwin (1995) suggested that recent increases in great blue heron populations resulted from this bird's practice of feeding in aquaculture ponds. Finally, regional monitoring of bird populations is essential because of geographic movements of species. For example, white ibis and wood stork populations have declined in south Florida but are stable in the Southeast as a whole because of population shifts northward to northern Florida, Georgia, and the Carolinas (Erwin 1995).

Mammals

Terrestrial and freshwater habitats in the Southeast are home to 101 mammal species (Echternacht and Harris 1993; Table 11). Of these, 5 are extirpated, all of them ecologically important species of either large carnivores or grazers: jaguar, ocelot, gray wolf, elk, and bison (Echternacht and Harris 1993). Two other large carnivores are on the verge of extinction: the Florida panther, the only remaining subspecies of mountain lion in the eastern United States, and the red wolf.

Endemic species represent a relatively small percentage of the mammals. According to

Echternacht and Harris (1993), eight small mammal species are endemic to the Coastal Plain province of the Southeast: southeastern pocket gopher, colonial pocket gopher, Sherman's pocket gopher, Cumberland Island pocket gopher, oldfield mouse, Florida mouse, Perdido Key beach mouse, and round-tailed muskrat. The region also has eight species of introduced mammals, four of which have many adverse effects on native communities: coyote, pig (feral domesticated pigs and wild boar) in the mountains and Coastal Plain, and nutria and horse in the Coastal Plain. Beavers were extirpated in the Southeast but have become reestablished in the last 20 years. Although beavers were historically important in the maintenance of habitat diversity, beavers of today inhabit landscapes with reduced predation and where the remnant habitats may themselves be vulnerable to loss from flooding.

There are 22 federally listed mammals in the Southeast: eastern mountain lion and the Florida panther, Key deer, gray wolf, red wolf, Louisiana black bear, 4 species of bats, 9 small mammal species restricted to the Coastal Plain in Florida or Alabama, a shrew restricted to Virginia and North Carolina, and 2 species of flying squirrels restricted to the mountains (Lee et al. 1982; Humphrey 1992). The eastern mountain lion and the gray wolf are already extirpated in the Southeast. In the following sections we discuss these and other species representative of trends in southeastern mammals.

Small Mammals

Small mammal species that are most at risk in the Southeast have narrow distributions. Most of the threats to these species come from development and subsequent loss of habitat. In isolated communities, such as beach habitats, feral cats represent a significant threat. Shrews and other insectivorous mammals suffer from the concentrated effects of residual pesticides. Fleming and Holler (1989) described ongoing efforts to reintroduce the endangered Perdido Key beach mouse to a site in Gulf Islands National Seashore.

The future of the fox squirrel is linked to that of its habitat, the longleaf pine savannah. A long-lived species with low reproductive rates, the fox squirrel has not been well studied or understood, but timbering, fire suppression, and development are all limiting its range and reducing its population sizes.

Bats

Of the 39 bat species listed for the United States, 17 occur in the Southeast (Di Silvestro 1989). Widespread pesticide use, resulting in poisoning as well as loss of food sources, is responsible for significant declines in bat populations since the 1960's (Di Silvestro 1989; Humphrey 1992; Drobney and Clawson 1995). This threat has diminished with regulations on pesticide use. The greatest threat to bats now comes from habitat destruction and disturbance. Few caves meet the temperature and humidity requirements bats need for hibernation, and these caves are occupied by large numbers of bats, making these bats particularly vulnerable to disturbance. The slow rate of reproduction among bats (often only one offspring per year) means that a population can be quickly destroyed, with little opportunity for recovery (Di Silvestro 1989).

The Indiana bat ranges over a huge area of the eastern United States, but the winter habitat for 85% of the species is limited to just seven caves, with over half of the population using just two caves (Di Silvestro 1989). Human disturbance has caused numbers of this species to drop from 330,000 to 49,000 in Kentucky alone (Di Silvestro 1989). Nationally, the decline in the Indiana bat population has reached 22% in the past 10 years (Drobney and Clawson 1995). Missouri has experienced the greatest decline (34%), whereas bat numbers in Indiana have somewhat increased and Kentucky's population is now stable.

The gray bat has suffered a similar fate. Guano collection during the Civil War caused heavy losses initially because of disturbances to nursery caves and habitats, but the gray bat recovered, only to be decimated by the popularity of cave exploration in the 1960's and 1970's. Between 1970 and 1976 the population of some colonies dropped more than 50%. Though only a handful of caves are suitable for the gray bat, this species is showing signs of recovery, largely due to the protection of four critical caves (Di Silvestro 1989).

River Otter

The river otter inhabits slow-moving streams, ponds, and other wetlands (Di Silvestro 1989). Historical threats included trapping and hunting. As a result of overtrapping in the 1970's, the otter was given protection through the Convention on International Trade in Wild Species of Endangered Flora and Fauna. Trapping pressure continues, however, as otters are frequently caught in traps intended for beaver.

The future of the river otter is inextricably linked to the future of wetlands, which are disappearing at the rate of 200,000 hectares per year (Di Silvestro 1989). Otter reintroduction programs are under way in Kentucky and Tennessee. Reintroduction in the Great Smoky Mountains National Park, where the otter population was completely extirpated by 1936, began in 1986. This program is showing some signs of success; juvenile otters are seen on a regular basis.

Wolves

The gray wolf has long been extirpated from this region. The red wolf, once a dominant predator of bottomlands and hardwood forests, was listed as endangered in 1967 and is now the focus of reintroduction programs (Rees 1989).

As the red wolf neared complete extinction in the mid-1970's, the remaining red wolves, reduced in range to the swamps of southern Louisiana, were captured to initiate a breeding program. Of the 400 animals captured, only 14 were considered true wolves; these became the basis of the breeding stock. Today there are 201 red wolves in captivity and about 80 in the wild; these were released in the Alligator River National Wildlife Refuge in eastern North Carolina, Great Smoky Mountains National Park, and protected areas on barrier islands of South Carolina, Florida, and Mississippi (G. Henry, U.S. Fish and Wildlife Service, unpublished data).

Red wolves have suffered from loss of habitat and intentional trapping, poisoning, and hunting. More recently, their greatest threat has been genetic dilution because of hybridization with wild dogs and coyotes, which have invaded the Southeast. A lack of mates may increase the chances of hybridization, so only mated pairs of red wolves have been released (C. Lucash, Great Smokey Mountains National Park, Gatlinburg, Tennessee, and University of Tennessee, Knoxville, personal communication).

Florida Panther

The Florida panther, the only subspecies of mountain lion remaining in the eastern United States, was once found throughout the southeastern Coastal Plain from Arkansas east to South Carolina (Humphrey 1992). This subspecies is now limited to the woodlands of the southern tip of peninsular Florida. Although other subspecies of mountain lion were extirpated by hunting and habitat loss in the early part of this century, the Florida panther's numbers were not only reduced by hunting but also by development, agricultural expansion, and degradation and fragmentation of habitat.

Today the Florida panther's numbers are estimated at between 30 and 50, and declining. Loss of habitat is the greatest threat the panthers face, as well as illegal shootings and highway collisions, which slowly remove more individuals than can be replaced naturally. Each individual loss represents a loss of genetic diversity, which results in inbreeding and increased numbers of abnormalities. Florida panthers are now estimated to have only half of the genetic diversity of western mountain lions (Humphrey 1992). The panther's continued presence in southern Florida is due to the existence of large interconnected blocks of public and private woodland and areas in successional stages, which support populations of deer and feral pigs, their most important prey (Humphrey 1992).

Scientists and resource managers have taken many measures to preserve the remaining Florida panthers. Highway underpasses, constructed for panther migration, have shown signs of panther use. A captive breeding program began in 1991, with a goal of 130 breeding animals by the year 2000 (Fergus 1991). A vigorous public education program has resulted in the panther being named the state mammal by popular vote of Florida's school children (Humphrey 1992).

Key Deer

The Key deer is the smallest of the eastern races of white-tailed deer and is endemic to south Florida. Hunting in the early part of this century brought their numbers down to between 25 and 80 animals by 1951 (Humphrey 1992). After hunting was banned in 1939, the deer's numbers returned to nearly 400 by 1974. The numbers have since dropped again, however, as a result of habitat loss, illegal poaching, traffic accidents, attacks by feral dogs, and loss of freshwater supplies (Humphrey 1992).

White-Tailed Deer

White-tailed deer populations have fluctuated dramatically with changing human influence and land use. We can identify four periods of contrasting trends and influence on native ecosystems. Before 1500, deer populations were moderate in size—Native Americans hunted deer extensively, and large native predators of deer were also present. Between 1500 and 1800, deer populations probably increased in some areas and decreased in others. Increases occurred because of reduced hunting by Native Americans and the increase in old-field habitats as Native American farms and villages were abandoned after Europeans displaced the native populations. Decreases were the result of exploitive hunting for trade by Native Americans and European colonists. Between 1800 and 1930 deer populations were reduced to near extirpation in many areas because of increased hunting, widespread agricultural clearing, and also other causes such as draining of wetlands. Since 1930 deer populations have rebounded vigorously because of farm abandonment, lower hunting pressure, and the near-absence of natural deer predators. Deer populations are still increasing in the Southeast and in some areas are drastically altering the composition and density of understory stems in forests. Deer are a major issue in forest and conservation management.

Black Bear

Black bears once occupied the entire southeastern United States (Fig. 40). This omnivorous, intelligent, and adaptable carnivore can survive in a diversity of forested habitats. Over the past 150 years, however, intensive human activities, primarily urban development and land clearing for agricultural crops, have reduced the species to less than 10% of its former range (Fig. 40). Black bears have been virtually eliminated from the Piedmont physiographic region and now occur only in the Coastal Plain and in mountain areas of the Appalachians, Ouachitas, and Ozarks. Bears occur in the Coastal Plain from the Dismal Swamp in Virginia, along parts of the Atlantic and Gulf of Mexico coasts to Louisiana, and sporadically up the Mississippi River delta to the White River National Wildlife Refuge (Wooding et al. 1994; Vaughan and Pelton 1995). More than 80% of the high mountain habitat of black bears occurs on public lands, but coastal habitats are predominantly on private lands (77% private, including the holdings of large timber companies; M. Pelton, University of Tennessee, Knoxville, unpublished data).

Black bears in the Ouachita and Ozark national forests have a unique history. Before 1950 no bears remained in these large areas of northwestern Arkansas, southern Missouri, and eastern Oklahoma. In the 1950's, more than 250 black bears were trapped and translocated from Minnesota to the Ouachitas and Ozarks. Since then, the black bear population has expanded to more than 3,000 individuals. This success story is in contrast to the recent designation of the Louisiana and western Mississippi black bear population as threatened (U.S. Fish and Wildlife Service 1994). This population exists on remaining small tracts of bottomland hardwoods. Likewise, the Florida black bear is categorized as authorized for listing on the U.S. list of endangered and threatened species and may be listed soon. The Florida subspecies suffers from the same problems of bottomland hardwood loss to agricultural crops and expanding human populations.

Bear population health within the region ranges from good to questionable. In areas such as the southern Appalachians of Georgia, North Carolina, South Carolina, and Tennessee, more than 3,000 bears reside on four national forests, one national park, and some private lands; this area encompasses nearly 2.5 million hectares. Four hundred to 600 bears are legally harvested from this population annually. Almost 500,000 hectares of this land are in designated or de facto sanctuaries or refuges. On the other hand, on some sites in the Coastal Plain only 20 to 60 bears may exist in the relatively isolated bottomland hardwood tracts that remained after extensive clearing of forests for agriculture.

Managers have translocated black bears from occupied habitats to areas in which large blocks of forest occur. For example, an experimental black bear population has been reintroduced into the Big South Fork region in the Cumberland Mountains of Kentucky and Tennessee; so far, this experimental reintroduction has been successful. This area encompasses more than 80,000 hectares, consisting primarily of the Big South Fork National River and Recreation Area and the Stearns Ranger District of the Daniel Boone National Forest. In the Coastal Plain, researchers estimate that more than 1.5 million hectares of unoccupied, potential bear habitat exist.

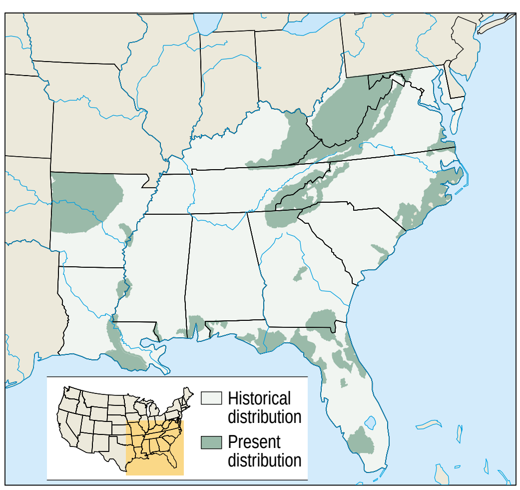

Fig. 40. Present distribution of the American black bear in the southeastern United States. Distribution is based on 1993 survey responses (M. R. Pelton, University of Tennessee, Knoxville, unpublished data).

Information Needs

We write at a time when the first attempts are being made to understand trends in the Southeast's rich biological diversity. Adequate information exists only for selected species and ecosystems—recent work on wetland loss provides the single best documentation of change at the ecosystem level. A number of endangered species are adequately monitored, but birds are the only widely distributed group for which there is a regular comprehensive regional monitoring program. Research has often focused on birds, but we are also much in need of regional inventory and monitoring schemes for other groups that play critical ecosystem roles, such as fungi (Mueller 1995; Rossman 1995), or are likely indicators of environmental change, such as lichens (Bennett 1995), amphibians, mussels, butterflies and moths (Powell 1995), and diatoms (Charles and Kociolek 1995).

Even in the best cases, however, spatial and temporal variability can make detection of trends difficult, as we have recently seen with attempts to detect trends in amphibian populations. Monitoring must be carried out in a regional and national context. For example, spatial shifts in bird populations have shown us that species can increase in one area and decrease in another (Erwin 1995). Such shifts are even to be expected if climate change occurs. Clearly, we must do a better job of monitoring so that we will be able to describe, understand, and predict trends.

Although the potential loss of a species is so dramatic that it attracts our attention, the single-most important regional trend is one that is occurring around us all the time but is rarely noted—the loss of populations and the fragmentation of range for species not yet endangered. There are many reasons to believe that this is a general phenomenon in the Southeast: changes in ecosystems due to fire suppression, outright conversion of natural habitat to forest plantations and agriculture, and changes in hydrology and water quality. Scientists presume that the loss of populations reduces genetic diversity, interrupts gene flow and dispersal, and destabilizes species originally dependent on metapopulation dynamics.

Biological monitoring should be developed in a way that allows us to address the ecological and landscape context of populations. Population change may be the result of such community properties as succession and the invasion of nonindigenous species or physical variables such as weather and pollutant exposure. Population change in one habitat may be the result of changes in another (for example, the loss of nearby wetlands). Although we may broadly monitor populations spatially, ecological and landscape variables also should be monitored, at least in intensively studied sites, if we are to understand the trends we detect.

Monitoring should include periodic mapping of ecosystems, ground-based monitoring of ecosystem dynamics, analysis of ecosystem processes, and simulation modeling for prediction. Work on the Everglades is perhaps the best example of a comprehensive and multidisciplinary approach to monitoring (Davis and Ogden 1994b). Other sites that have included several, if not all, of these elements are the southern Appalachian spruce–fir forests (Eagar and Adams 1992), Coweeta Hydrologic Laboratory (a National Science Foundation Long-Term Ecological Research site), and the Savannah River Ecology Laboratory.

Even in these areas, though, researchers often note the short period of data collection and the resulting difficulty of separating trends from natural fluctuation. The danger of inadequate information is the confusion and conflict that often occur when a loss of biological diversity is first suspected. To see this situation in the Southeast we need only turn back the clock some 15 years; when the first concerns about acid rain effects in the southern mountains were raised, there was little understanding of expected growth and mortality or of soil chemistry, ecosystem processes relating to nitrogen transformations, or fluctuation in streams that drained high-elevation watersheds. We must design monitoring and research strategies to deal with an ever-lengthening list of suspected regional trends in biological diversity such as the recent reported declines in Neotropical migrants, amphibians, and tree growth rates.

We also argue for a bioregional approach to monitoring and research: intensive multidisciplinary work on regional landscapes. Such an approach is used in the Everglades, Chesapeake Bay (Pendleton 1995), the Appalachicola River basin (Livingston 1992), the Savannah River Ecology Laboratory, and the Biosphere Reserve programs in the southern Appalachians, the Mammoth Cave area in Kentucky, and the Land-Between-the-Lakes region in Tennessee. All of these projects not only include strictly preserved areas but also recognize the inevitable presence of humans in the Southeast and seek to protect biological diversity while allowing some areas to be intensively used by people. These projects also include multiple public and private partners.

We critically need better information on a range of key issues that will help us maximize the biological diversity that can persist in the Southeast. These issues include better understanding of

- the sensitivity of species to habitat fragmentation and the persistence of species in agricultural landscapes of various types;
- the roles of hydrological regimes and fires of various intensities and in different seasons;
- the ways to avoid future nonindigenous species problems and to control the problems that already exist;
- sustainable methods and levels of harvest, both for target species and for nontarget species that are affected by harvest;
- the ways to propagate species taken directly from the wild to avoid damage to surviving natural areas;

Authors

Peter S. White
Department of Biology and North Carolina Botanical Garden
University of North Carolina at Chapel Hill
Chapel Hill, North Carolina 27599

Stephanie P. Wilds
Gwendolyn A. Thunhorst
Curriculum in Ecology
University of North Carolina at Chapel Hill
Chapel Hill, North Carolina 27599

Contributing authors

John M. Alderman
North Carolina Wildlife Resources Commission
Pittsboro, North Carolina 27312

Matthew Barnett-Lawrence
North Carolina Botanical Garden
University of North Carolina at Chapel Hill
Chapel Hill, North Carolina 27599

J. Whitfield Gibbons
Savannah River Ecology Laboratory
University of Georgia
Aiken, South Carolina 29802

Thomas C. Gibson
Department of Botany
University of Wisconsin
Madison, Wisconsin 53706

David S. Lee
North Carolina Museum of Natural Sciences
Raleigh, North Carolina 27626

Michael R. Pelton
Department of Forestry, Fisheries, and Wildlife
University of Tennessee
Knoxville, Tennessee 37901

David Penrose
North Carolina Department of Environment, Health, and Natural Resources
Raleigh, North Carolina 27607

James D. Williams
U.S. Geological Survey
Biological Resources Division
Florida Caribbean Science Center
7920 N.W. 71st Street
Gainesville, Florida 32653

- the ways to develop off-site gene and species banks as last resorts for the rarest and most threatened species;
- the ways to restore natural processes and whole systems on the ubiquitous degraded lands in the Southeast;
- and the ways to predict the varying sensitivities of ecosystems and species to sea-level rise and climatic change.

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