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9

Pine Flatwoods and Xeric Pine Forests of the Southern (Lower) Coastal Plain

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The southeastern Coastal Plain begins in Virginia and includes parts of North Carolina, South Carolina, Georgia, Alabama, Mississippi, Louisiana, Texas, and all of Florida. A great diversity of aquatic, terrestrial, and transitional biotic communities exist within this varied landscape. The interplay between soils, elevation, and drainage is manifested in numerous environmental gradients along which the biota separates itself in space and time into superficially redundant species assemblages. Diversity within habitats (alpha), between habitats (beta), and across landscape gradients (gamma) portended conflict between development, resource management, and conservation of this diversity.

Historically, the Coastal Plain was naturally forested and these forests fell into two types: pinewoods and swamps (forested wetlands). Thus uplands and wetlands were juxtaposed over short longitudinal distances (a few meters) by slight differences in elevation (a few centimeters). Hardwood forests were scattered in the largely pine-dominated landscape and revealed the potential of the uplands to support other communities with changes in disturbance regimes (Quarterman and Keever 1962).

The paleobotanical history of the vegetation of the Coastal Plain has been described by Delcourt and Delcourt (1977, 1981) (see Chapter 2 in this volume). Global climatic changes resulted in a series of complete and partial inundations by sea-level rises and more recently reductions of sea level with concomitant increases in areas of coastal land. Dramatic changes in climate, sea level, and water tables were associated with shifts in plant community species composition and the dependent fauna. Watts and Hansen (1988) suggested extant lakes and freshwater

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wetlands have developed in the last 5000 years within peninsular Florida. The megafauna of the Coastal Plain disappeared in the interval between 3000 and 18,000 years before present (YBP) (Webb 1990). Coastal Plain biotic communities as we understand them have originated in the last 5000–10,000 years. Humans have been a part of these natural systems throughout this relatively brief history; Europeans have been present in the Coastal Plain for nearly 500 years.

We review the historic and recent knowledge of pine communities of the southeastern Coastal Plain with emphasis on their classification, structural attributes, dynamics, and resource management. The uneven attention of past research on these communities limited the descriptive details that may be provided on each community and pointed to research needs of the future.

Our review is a companion to Chapter 10. We emphasize the pine ecosystems of Florida: pine flatwoods, longleaf pine–turkey oak sandhills, sand pine scrub, scrubby flatwoods, and subtropical pine forests. Of these, Küchler (1964) recognizes the sand pine scrub of central Florida and the subtropical pine forests of south Florida (Fig. 1). We provide maps of flatwoods and longleaf pine–turkey oak communities. They are more extensive than sand pine scrub and subtropical pine forests, but Küchler (1964) includes them within the Southern Mixed Forest. This chapter and Chapter 10 show that such a classification greatly oversimplifies the complex vegetation structure and history on the lower Coastal Plain.

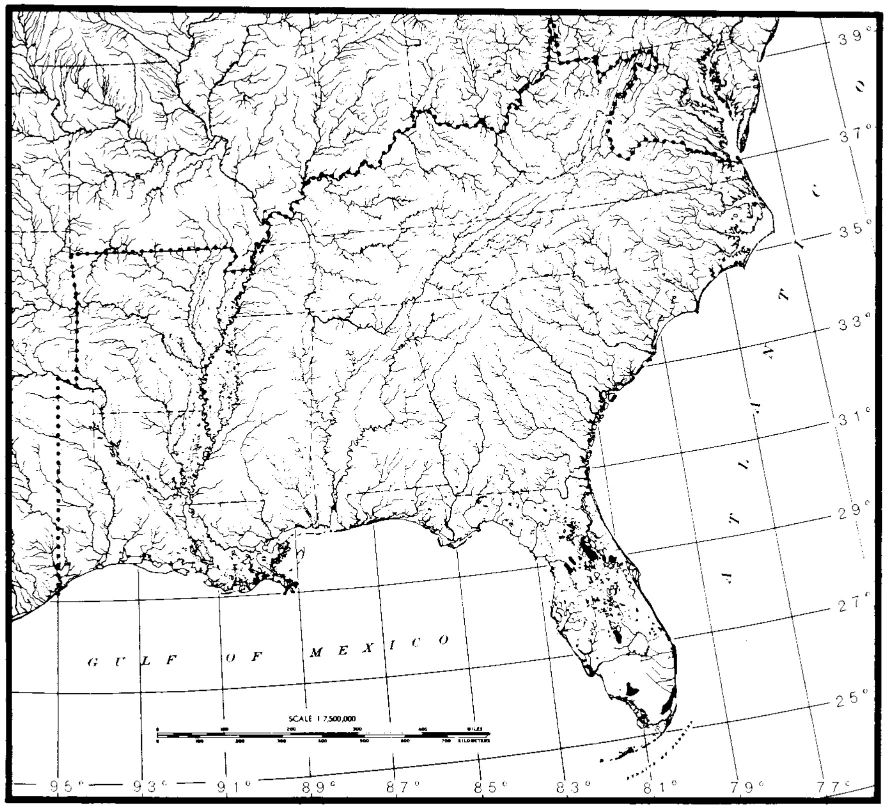

FIGURE 1. Pine communities recognized by Küchler (1964) in peninsular Florida. Sand pine scrub (Type 115) in central Florida and subtropical pine forest (Type 116) in southern Florida.

THE PHYSICAL ENVIRONMENT

Geography and Physiography

Pinelands of the southeastern United States historically extended from extreme southeastern Virginia southward through the Carolinas, Georgia, and Florida and westward into Alabama, Mississippi, and Louisiana to reach Texas east of the Trinity River. This region spans 12 degrees latitude (25–37° N) and 20 degrees longitude (75–95° W) and is embedded within the Atlantic and Gulf Coastal Province, which includes 1,851,000 km^2 (Walker and Coleman 1987).

These pineland communities occupied substrates derived from geomorphic processes dating to the Cretaceous (70–135 MYBP), but more typically from the Tertiary and Quaternary periods (2–70 MYBP). All have shared a history of influences from sea-level variations and attendant variations in aridity. In addition, all these pinelands shared pyrogenic origins (Komarek 1968, 1974) with fire adaptation as a common nexus among communities and species.

The Atlantic and Gulf Coastal Province has a long history of submergence and emergence events. During the last glaciation the emerged portion of the province was much greater due to eustatic sea-level reduction. Most of the province has been emergent since the Cretaceous (Walker and Coleman 1987). For the last 5000 years the present stand of the Gulf of Mexico and the Atlantic Ocean has marked the seaward limits of the pinelands; northward other provinces (e.g., the Piedmont Plateau, Valley and Ridges, and Appalachian Plateau) limit the Coastal Plain. Local relief is modest with more than half of the region under 30 m and the more extreme topography in the range of 30–90 m. Because of historic erosion and subsidence, the slight relief of the Coastal Plain supports extensive riverine wetlands (Wharton et al. 1982), whereas karst-lake topography characterizes portions of peninsular Florida (White 1970, Webb 1990).

Special physiographic features of the Coastal Plain include the peninsula of Florida and the valley of the Mississippi River. Much of the southeastern Coastal Plain borders the Piedmont Plateau along the fall line, a region where streams exhibit rapids and waterfalls before descending into the Coastal Plain and its shallow valleys.

Major Drainages

The low local relief of the Atlantic and Gulf Coastal Province gives rise to many slow meandering rivers that discharge into the Atlantic Ocean or the Gulf of Mexico. Many of the major rivers arise in the highlands of neighboring geomorphic provinces and flow across the Coastal Plain, often perpendicular to the shoreline (Table 1). In Florida, only the Apalachicola arises outside the Coastal Plain. The drainage area of rivers reaching the Coastal Plain is 5.5 × 10^6 km^2 and nearly 21% of this area is within the Coastal Plain itself (Walker and Coleman 1987). The Mississippi River is a dominant feature because of drainage area, total discharge, and amount of sediment carried to the Continental Shelf. Forty-two major streams reach the coast from the area of the Coastal Plain that supports pinelands. These streams arise from 13 major drainage areas that may include several river basins within a drainage area (Walker and Coleman 1987).

Climate

The climate of the Atlantic and Gulf Coastal Plain is characterized by warm summers and mild winters. Yearly mean air temperature ranges from about 15.5°C in North and South Carolina, to 18.8°C in Louisiana, to the high of 22.8°C at Homestead, Florida (Ruffner 1985). January temperatures reflect a gradual reduction in "normal" daily values from 21.2°C in extreme south Florida to about 4.5°C in southeast Virginia (Nelson and Zillgitt 1969). The freeze-free period averages 330 days within the range of rockland pinelands in south Florida to about 240 days at the limit of Coastal Plain pinelands dominated by longleaf pine (*Pinus palustris*). Yearly mean precipitation varies from 114 cm at 30.5 m elevation in Dillon, South Carolina, to 162 cm at 54.8 m elevation in Amite, Louisiana (Ruffner 1985). Within the Coastal Plain, the states bordering the Gulf of Mexico tend to receive higher rainfall than the Atlantic coastal states. Climatic conditions throughout the Coastal Plain provide a physical basis for the development of highly weathered, leached, acid soil low in natural fertility, particularly in the uplands (Fiskell and Perkins 1970).

TABLE 1 Major Rivers of the Southeastern Coastal Plain

River	Drainage Area in Coastal Plain (km^2)	(%)
Cape Fear	11,800	51
Pee Dee-Yadkin	17,100	42
Santee	9,200	21
Savannah	7,900	29
Altamaha-Ocmulgee	20,700	57
Suwannee	25,100	100
Apalachicola	29,700	64
Tombigbee-Alabama	62,500	55
Pearl	21,700	100
Mississippi	302,000	9
Sabine-Neches	54,400	100
Trinity	40,400	92

Source. Adapted from Table 3 in Walker and Coleman (1987).

Geology and Soils

The Atlantic and Gulf Coastal Plain is elevated, former sea bottom formed at the trailing edge of the North American Plate during Mesozic and Cenozoic Eras that extends inland from 160.9 to 321.8 km (Hunt 1974, Walker and Coleman 1987). Consistent with the sea bottom origin, geological formations are sedimentary in origin and date to the beginning of the Cretaceous. Thus Cretaceous, Tertiary, and Quaternary geological formations underlie the Coastal Plain and represent the seaward (outward) deposition of sediments coupled with local upward movements of the bedrock. The bedrock is Precambrian and Paleozoic in age; a well near the tip of Florida was found to have traversed 11,600 ft (3.5 km) of sedimentary deposits before reaching basement rock (Thornbury 1965). Basement rock includes metamorphic, igneous crystalline, and sedimentary rock dating to the Triassic and Paleozoic times (Murray 1961, Hunt 1974, Walker and Coleman 1987).

The inner boundary of the Coastal Plain is marked by the fall line, where the basement rocks rise beneath Cretaceous and Tertiary formations. Rivers passing the fall line exit the Piedmont Plateau through a series of rapids and falls before widening and slowing in the Coastal Plain. Fall line hills are sandy and slightly higher than the older Piedmont Plateau. These hills were derived from Tuscaloosa and Eutaw Formations of Upper Cretaceous age. Norfolk soils 22.2–24.3 m in depth blanket these uplands. These soils are well drained and acidic in reaction (Stringfield 1966). The fall line ends in central Alabama where the Coastal Plain meets the Appalachian Highlands.

The entire Coastal Plain was submerged during Cretaceous times (Kennett 1982). A geological cross section perpendicular to the coastline through South Carolina would reveal the following layers, each progressively older in the landward direction: (1) Quaternary, (2) Upper Tertiary (Miocene and Pliocene), (3) Lower Tertiary (Paleocene, Eocene, Oligocene), (4) Cretaceous, and (5) Paleozoic (some Precambrian and Triassic) (Hunt 1974). Part of the present land has been emergent throughout the Cenozoic (Tertiary and Quaternary periods) or for the past 70,000,000 years. Land area has been stable for the last 5000–6000 years (Walker and Coleman 1987). Surface features have been modified by erosion and/or burial during successive periods of submergence and emergence.

Pinelands of the southeastern Coastal Plain occur on lower and upper Tertiary and Quaternary sedimentary deposits. Most of these formations accumulated during periods of submergence; however, fluvial and eolian deposits do occur (Walker and Coleman 1987). Lower Tertiary sediments are largely marine limestone and sand. Upper Tertiary sediments extend nearly the full length of Florida and include marine sand, clay, and marl and much of the limestone of Florida (Stringfield

1966, Walker and Coleman 1987). Quaternary deposits are extensive along the coast and consist mainly of riverine gravel, sand and clay, marine limestone, and eolian loess.

The Tertiary and Quaternary deposits exhibit seaward inclines that have been modified by warping and faulting (Walker and Coleman 1987). Notable uplifts within the region include the Cape Fear and Ocala Arches. The Ocala Arch represents an anticlinal ridge that extends from south Georgia to central Florida (Walker and Coleman 1987). This uplift, approximately 112.6 km wide and 370 km long, developed in Tertiary sediments. Eocene Ocala limestone is 45.7 m above sea level (Thornbury 1965). Cretaceous limestone and shale more than 3 km thick make up the bedrock of most of the Florida peninsula (Hunt 1974). Karst processes have resulted in numerous sinkhole lakes in this region. Caverns in the limestone are continuous with aquifers and tend to be water-filled in central Florida; air-filled caverns are present in north Florida (Thornbury 1965). Karst terrain is a prominent feature of the southeastern Coastal Plain from North Carolina to eastern Mississippi; however, sinkhole ponds and lakes are restricted to Florida (Walker and Coleman 1987).

Quaternary formations were still submerged during the Pleistocene in coastal Texas, Louisiana, Mississippi, Alabama, Florida, Georgia, and North Carolina (Kennett 1982). Coastal Plain terraces have long been a subject of controversy with regard to age (Cooke 1945, MacNeil 1950, Alt and Brooks 1965). It is now certain that terraces of the same sea-level stand may be at different elevations owing to emergence and subsidence events (Opdyke et al. 1984, Walker and Coleman 1987). Florida is unusual in that much of its surface consists of former marine terraces (Thornbury 1965, Brown et al. 1990).

Surface deposits on the Coastal Plain include sand and gravel on the uplands, alluvium in the river floodplains, and a limited amount of loessial deposits east of the Mississippi River (Hunt 1974). Most of these deposits are of Holocene origin and the soils are poorly developed. Histosols (peat and muck) are the most recent in origin (Buol 1973). Slightly older soils are the Spodosols formed on sandy Quaternary formations with poor drainage. These soils have organic and iron-rich spodic layers beneath surface layers that vary in thickness from a few centimeters to several decimeters. Such soils were derived from marine deposits late in the Pleistocene or the early Holocene period. Pine flatwoods are associated with these Spodosols on coastal terraces (Brown et al. 1990). In contrast, the deep sandy Entisols support longleaf pine–turkey oak sandhills in South Carolina, Georgia, and Florida (Buol 1973). Sand pine scrubs of Florida are also found on Entisols.

The south Florida basin received large amounts of sediment during the Cretaceous (Walker and Coleman 1987). This land emerged somewhat over 5000 years ago and represents a former sea bottom in Pliocene time. Decline of sea level exposed limestone and marl in the late Wisconsin time (Thornbury 1965) and allowed the Everglades to begin to develop.

Miami rock ridge forms the eastern boundary of the Everglades. Here the Plio-Pleistocene Caloosahatchee and Pleistocene Anastasia formations form the highest ridgeland in Palm Beach County (Brooks 1968, Gleason et al. 1974). The ridge continues south into Everglades National Park as Long Pine Key. The oolitic limestone disappears and sediments of Holocene origin continue into Shark Valley, where sawgrass prairie dominates. Oolitic limestone reappears in the Lower Keys along with subtropical pinelands (Brown et al. 1990). On the western margin of the Everglades, two formations, Caloosahatchee and Tamiami, extend north–south from Lake Okeechobee to the Gulf of Mexico. Unconsolidated sands dating from the highest Pleistocene sea-level deposits cover these bedrocks (Gleason et al. 1974). Entisols, Alfisols, and Mollisols may be developed in association with subtropical pinelands (Brown et al. 1990).

The Atlantic Coastal Ridge, a system of relict beach ridges and bars, runs along the entire east coast of Florida to disappear near Homestead, southwest of Miami. These marine sand deposits have been considered a result of Pamlico time when the sea level was about 9.1 m higher (White 1970). Much of these highly washed and sorted marine sands include Paola, St. Lucie, Jonathan, Pomello, and Satellite soils. Sand pine scrub typically vegetated these coastal features.

VEGETATION

The potential terrestrial vegetation of the southeastern Coastal Plain was included within the Eastern Deciduous Forest Region by Clements (1916); however, Weaver and Clements (1938) classified the vegetation as a fire subclimax within the Eastern Deciduous Forest. Braun (1950) further modified the terminology to Southeastern Evergreen Forest Region of the Eastern Deciduous Forest to highlight the broadleaf evergreen nature of many of the trees. The seminal work of Quarterman and Keever (1962) resulted in their recognition of the Southern Mixed Hardwood Forest (= an association) with dominance shared among 14 species of trees and no clearly defined association segregates. A lack of recurring fires allowed a variety of seral pinelands to be succeeded by the abstract Southern Mixed Hardwood Forest on mesic sites. Shelford (1963) treated the eastern half of North America as the Temperate Deciduous Forest Biome with two subdivisions: (1) Northern and Upland Region and (2) Southern and Lowland Region. Pinelands within the latter region were separated as flatwoods, pinelands (sand pine scrub included here), and the Longleaf Pine–Turkey Oak–Wiregrass–Pocket Gopher Community. Daubenmire (1978) treated the eastern United States as the Temperate Mesophytic Forest Region. His *Quercus flacata* Province, central and southern sections, embraced the pinelands of interest here.

As clearly stated by Monk (1965, p. 349), the vegetation of the southeastern Coastal Plain is dominated by pinelands based on area occupied. Nevertheless, the Southern Mixed Hardwood Forest may be defended as a regional "stable type" community on mesic zonal soils. This leaves the more extensive pinelands to be classified. The viewpoint taken here is allied with the polyclimax theory of Tansley (1935) and accepts the pinelands as disturbance-dependent pyrogenic "stable types." The potential natural vegetation of the southeastern United States as mapped and defined by Küchler (1964) provides a convenient starting point to build upon in presenting these pineland biotic communities. The Küchler types to be treated in this chapter are portions of the area recognized as Southern Mixed Forest, Sand Pine Scrub, and Subtropical Pine Forests.

Potential Natural Vegetation

Southern Mixed Forest The Coastal Plain of the southeastern United States is classified as Southern Mixed Forest by Küchler (1964; Type 112), dominated by *Fagus-Liquidambar-Magnolia-Pinus-Quercus*. The vegetation that coincides with the geographic area is described in Chapter 10 in this volume. Under natural fire regimes, these forests were restricted to sites topographically protected from fire, such as slopes, islands, and peninsulas (Daubenmire 1990). Vast areas within this forest region are regarded as fire-dependent stable types and communities dominated by species of pine are widespread. Most prominent among these pinelands in Florida are pine flatwoods (*Pinus-Aristida*) and longleaf pine–turkey oak sandhills (*Pinus-Quercus laevis*) communities. In this discussion, we use the term "flatwoods" in the broader sense, not just for less well-drained sites characterized by slash pine (*Pinus elliottii*).

Pine Flatwoods Pine flatwoods represented the major forest type of the southeastern Coastal Plain in pre-Columbian times (Sargent 1884). About 50% of peninsular Florida was pine flatwoods (Davis 1967) (Fig. 2). Three major species of pines sorted out on topoedaphic gradients to yield communities dominated by longleaf pine on mesic sites (pH > 4.5), slash pine on slightly wetter sites (pH < 4.5) and near the coast, and pond pine (*Pinus serotina*) (Woodwell 1958, Edmisten 1963, Monk 1968). Fire frequency controlled stand characteristics at the local scale of resolution and in a general way across regional gradients. Forested and nonforested wetlands were scattered throughout the pine flatwoods and were functionally related to these systems through hydrologic and trophic processes.

Edmisten (1963) reviewed the history of pine flatwoods. He cited Small (1929) as having a reference to fire and pine flatwoods from 1580. Bartram (1791) discussed fire in the barrens (pine flatwoods) of north Florida. Early in this century, Harper described pine flatwoods of north-central Florida, central Florida, and south Florida (Harper 1914, 1921, 1927). Elsewhere, pine flatwoods were described by Wells (1928) in North Carolina and Wright and Wright (1932) in Georgia. Heyward (1939), Laessle (1942), and Garren (1943) established the critical role of fire in the maintenance of pine flatwoods and in the life cycle of longleaf pine.

Pine flatwoods occupy extensive "flats" or terraces that were shallow coastal waters associated with former shorelines of the Pleistocene Epoch. Thick beds of sands were deposited in these flat areas; subsequently, spodic horizons (hardpans) were formed by leaching and accumulation of organic matter, aluminum, and iron (U.S. Department of Agriculture, 1975). Hardpans are relatively impervious to water, and saturated soils and seasonal flooding are characteristic of pine flatwoods.

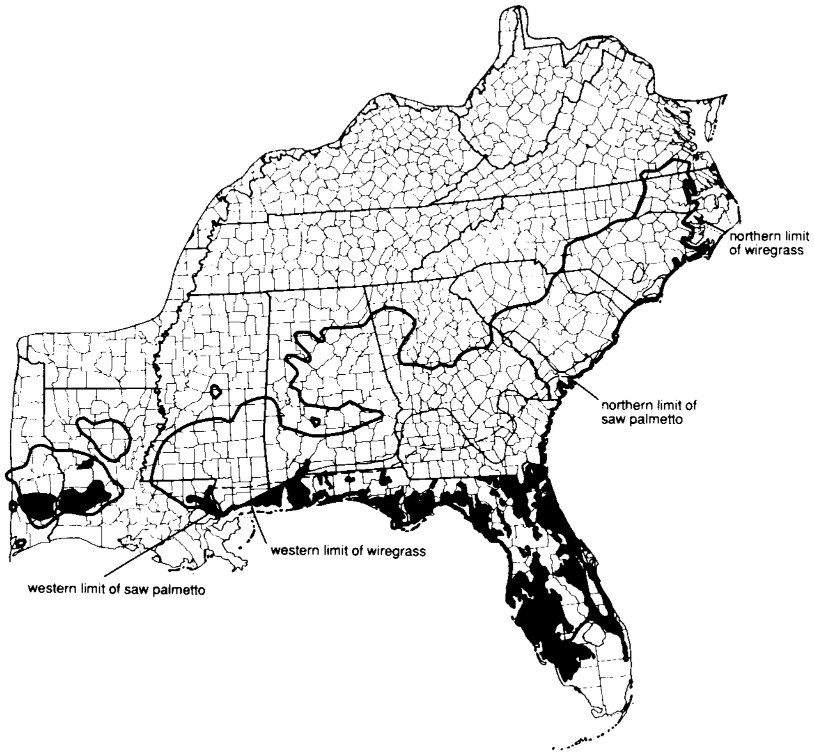

FIGURE 2. Distribution of pine flatwoods in the Coastal Plain of the southeastern U.S. A heavy, continuous line outlines the distribution of longleaf pine (Critchfield and Little 1966). A continuous line indicates the landward extent of wiregrass and the western and northern limits of its distribution. A broken line indicates the northern limit of saw palmetto (McNab and Edwards 1980). Shaded areas show regions of historic concentration of pine flatwoods. Shaded areas in Florida delimit landscapes dominated by pine flatwoods as mapped by Davis (1967).

Pinelands, including pine flatwoods dominated by longleaf pine (Fig. 3) once occupied 25 million ha of the southeastern Coastal Plain, stretching from southeast Virginia to Florida and westward to Texas (Sargent 1884, Fowells 1965, Davis 1967, Platt et al. 1988a). In general, longleaf pine dominated upland, moderately to poorly drained sites, where fire frequency was at 1–3 year intervals. Often down slope of the longleaf pine, slash pine gained dominance as the hydroperiod increased. Slash pine begins to dominate over longleaf pine in a transitional zone that crosses the Florida Peninsula north of Lake Okeechobee (Sargent 1884, Little 1978). Slash pine reaches the Florida Keys in other pineland types. Pine flatwoods dominated by either longleaf pine or slash pine were present in the Coastal Plain of Alabama, Mississippi, and eastern Louisiana. Only longleaf pine occurred in central and western Louisiana and extreme southeastern Texas. Likewise, only

FIGURE 3. Virgin forest of longleaf pine (*Pinus palustris*), photographed by Dr. E. A. Smith and R. S. Hodges in 1902 near Fairhope, Baldwin County, Alabama (Harper 1928).

longleaf pine occurred in pine flatwoods north of Georgetown County, South Carolina, the northern limit of slash pine's natural distribution (Fowells 1965).

Longleaf pine is a keystone species in pine flatwoods, sandhills, and pine savannas. It occurred in monospecific stands over a larger area than other tree species in presettlement landscapes (Sargent 1884, Platt et al. 1988a, Chapter 10, this volume). This was the result of a series of life history traits evolved in an environment characterized by moderate annual temperatures, abundant rainfall (much of which was associated with summer lightning storms), and frequent ground fires (Wahlenberg 1946, Fowells 1965, Christensen 1981, 1986). Given predictable and frequent ground fires (1–3 year intervals), the continued dominance by longleaf pine depended on the establishment and survival of seedlings and saplings in the openings that appeared within continuous stands of conspecifics. Fires were too intense in the duff beneath adult pines for young pines or oaks to survive (Williamson and Black 1981). A detailed study by Platt et al. (1988a) demonstrated that the size, age, and spatial structure of a longleaf pine forest were consistent with the hypothesis that a suite of pyrogenic traits (e.g., seedling resistance to fire injury, rapid height growth of saplings, and large annual needle cast by adults) favored the pine's survival over co-occurring hardwoods.

Slash pine and pond pine occupy wet depressions in pine flatwoods, which burn less frequently than do longleaf pine stands (Edmisten 1965, Abrahamson and Hartnett 1990). Larger individuals of both species are fairly resistant to "cool" ground fires. Neither species has a fire-resistant "grass" stage as found in longleaf pine (slash pines in extreme south Florida do, however). Fire may be more destructive, although at longer intervals, in pond pine stands where the close spacing of individuals may allow a ground fire to become a crown fire and thereby destroy the adults. Pond pine is, however, partially serotinous and depends on periodic disturbance to maintain stand dominance (Fowells 1965).

Christensen (1986) concluded the classification of flatwoods was intractable based on available information. Early classification of flatwoods in north Florida yielded longleaf pine–scrub oak and longleaf pine–saw palmetto associations (Gano 1917). Harper (1927) used the term "flatwoods" to identify communities dominated by slash pine and saw palmetto (*Serenoa repens*) growing on poorly drained sandy soils with little or no relief, a common usage on the Coastal Plain. The longleaf pine belt (southeastern half of Georgia, northern half of Florida, southern half of Alabama, Mississippi, and Louisiana, and the southeastern portion of eastern Texas) was reported to contain five different forest associations, one of which, the mesohydrophytic forest, was referred to as the longleaf–slash pine association (Pessin 1933). Flatwoods of the Welaka Area, northeast Florida, were described by Laessle (1942) as of three types: (1) longleaf pine–wiregrass association, (2) pond pine–fetterbush association, and (3) slash pine association. Monk (1968) modified Laessle's classification by treating the pine flatwoods complex as having three phases dominated by either longleaf pine, slash pine, or pond pine. In southeastern Florida, Richardson (1977) identified pine flatwoods dominated by slash pine and two subdivisions, scrubby flatwoods (treated elsewhere in this chapter) and low pine flatwoods (*Pinus elliottii–Aristida stricta*). Two types of pinelands in Georgia may be identified with flatwoods: (1) mesic pine lowland forest and (2) longleaf pine upland forest (Wharton 1978). Abrahamson et al. (1984) noted that the flatwoods association formed a continuum at the southern end of the Lake Wales Ridge. Nonetheless, five distinct phases were recognized: (1) wiregrass flatwoods, (2) cutthroat grass (*Panicum abscissum*) flatwoods, (3) palmetto flatwoods, (4) gallberry (*Ilex glabra*) flatwoods, and (5) fern–slash pine (*Woodwardia virginica* and *Osmunda cinnamomea*/*P. elliottii* var. *densa*) flatwoods. Based on floristic relationships, Bridges and Orzell (1989) identified three subtypes of wetland longleaf pine savanna in the West Gulf Coastal Plain of Louisiana and Texas. Abrahamson and Hartnett (1990) have summarized the ecological literature on pine flatwoods in Florida.

The physiognomy of classic pine flatwoods is characterized by an emergent tree layer of pines with limbless lower trunks, and a ground layer of low vegetation that appears homogeneous and species poor (Fig. 3). In spite of this appearance, total plant species richness tends to be high and careful collecting may reveal in excess of 100 species in a local area (Platt et al. 1988b, Bridges and Orzell 1989).

Tree species richness of pine flatwoods increases from south (2) to north (10) in peninsular Florida and this richness is maintained to the western limit of the community type in eastern Texas (Table 2). Only one or two tree species were present in stands on the southern Lake Wales Ridge (Abrahamson et al. 1984) and in longleaf, slash, and pond pine-dominated stands studied by Stout (1979) in east-central Florida. Monk (1968) reported 42 tree species in 32 stands of pine flatwoods from north-central Florida with an average of 10 species per stand. Hebb

TABLE 2 Composition of Individual Stands of Representative Pine Flatwoods from Florida to Texas

Species	Communities[a]						
	Southern Florida[b]			North-central Florida[c]	North Florida[d]	South-east Texas[e]	
Pine							
Pinus echinata							X
Pinus elliottii	X	D	D	D	X		
Pinus palustris				D		D	D
Pinus taeda						X	X
Oak							
Quercus echinata						X	
Quercus falcata						X	X
Quercus geminata		X					
Quercus incana						X	
Quercus laurifolia				X			
Quercus marilandica						X	
Quercus minima	X						
Quercus nigra				X		X	
Quercus stellata						X	
Quercus virginiana				X	D		X
Others							
Acer rubrum				X			
Andropogon sp.	X		X				
Aristida stricta	D		X				
Befaria racemosa			X				
Cyrilla racemiflora					X		X
Garberia fruticosa		X					
Hypericum reductum	X						
Ilex coriacea					X		
Ilex glabra		X	D				
Liquidamber styraciflua				X		X	X
Lyonia ferruginea				X			
Lyonia lucida	X	X	X				
Magnolia virginiana				X	D		X
Myrica cerifera				X		X	
Nyssa sylvatica				X	D		X
Panicum abscissum			D				
Persea borbonia		X			X		
Rhus copallina		X					
Serenoa repens	X	D	D				
Vaccinium myrsinites			X				
Ximenia americana		X					

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[a] Status within stands scored as dominant or codominant (D) or typical component (X) based on coverage, presence, or basal area.

[b] Composition of wiregrass (column 1), palmetto (column 2), and gallberry (column 3) phases of pine flatwoods, southern Lake Wales Ridge region. Adapted from cover data (>5%) (Abrahamson 1984).

[c] Tree species composition of pine flatwoods in north-central Florida; frequency >25%; from 32 communities (Monk 1968).

[d] Tree species composition of an old-growth slash pine stand, panhandle of Florida; basal area from trees > 5 cm DBH (Hebb and Clewell 1976).

[e] Tree species composition of upland pine forest (column 6) and wetland pine savanna (column 7), southeastern Texas; basal area values > 0.05 m^2/ha (Marks and Harcombe 1981).

and Clewell (1976) listed six tree species from old growth slash pine in the Florida Panhandle. At the western limit of longleaf pine forest in southeast coastal Texas, a minimum of 13 tree species were found in five stands (Marks and Harcombe 1981).

A great diversity of shrubs is found in the understory of pine flatwoods. Notable species include *Ilex glabra*, *Vaccinium myrsinites*, *Lyonia lucida*, *Quercus minima*, *Q. pumila*, *Q. geminata*, *Kalmia hirsuta*, and *Myrica cerifera* (Wharton 1978, Huck 1987). Saw palmetto yielded high cover values in four Florida counties where pine flatwoods were sampled (Tables 2 and 3). In the absence of frequent ground fires, *Q. geminata*, *Myrica cerifera*, and *Ilex cassine* grow rapidly to small tree size.

Fire-adapted plant communities tend to have a rich assemblage of grasses and herbs (Platt et al. 1988b). Grasses and herbs were not particularly common in wiregrass (12), palmetto (8), and gallberry (7) phases of pine flatwoods, which were dominated by woody species (Table 2, columns 1-3). Thirty-four species of grasses and herbs were identified in pine flatwoods in Orange County, Florida (Table 3). In contrast, Platt et al. (1988b) identified 147 forb species (excluding

TABLE 3 Composition (% Cover) of Understory of Two Phases of Pine Flatwoods Vegetation from Three Counties in East-Central Florida

	Longleaf Pine–Wiregrass Phase	Slash Pine–Palmetto Phase	
Species[a]	Orange County	Volusia County	Brevard County
Serenoa repens	41.7	23.0	37.6
Aristida spiciformis	23.2	—	—
Aristida stricta	20.9	12.6	3.2
Lyonia fruticosa	2.4	—	3.3
Asimina reticulata	1.9	—	—
Andropogon virginicus	2.9	—	—
Panicum ensifolium	1.4	—	—
Quercus minima	4.4	—	—
Lyonia lucida	1.7	7.6	14.3
Quercus pumila	1.6	—	—
Quercus myrtifolia	—	35.2	11.6
Quercus geminata	—	2.8	13.7
Gaylussacia dumosa	—	18.5	—
Quercus chapmanii	—	9.6	2.9
Ilex glabra	—	1.8	1.1
Myrica cerifera var. *pusilla*	—	1.3	4.0
Vaccinium myrsinites	—	—	4.6
Befaria racemosa	—	—	3.6
Pteridium aquilinum	—	—	1.2
Vitis rotundifolia	—	—	1.5

Source. Stout (1979).

[a] Species with cover >1%; total understory species present: Orange—49; Volusia—30; Brevard—31.

grasses and sedges) flowering on experimentally burned longleaf pine flatwoods plots (N = 17, each 500 m^2) sampled seven times over an annual cycle. Wiregrass (*Aristida stricta*) was a predictable grass in longleaf pine forests and savannas east of Mississippi, whereas flatwoods to the west were rich in grasses of the genus *Andropogon* (Grelen and Duvall 1966). Conspicuous herbs of pine flatwoods include several species of *Asclepias* spp., *Aster reticulatus*, *Carphephorus odoratissimus*, *Liatris* spp., *Stillingia sylvatica*, *Baptisia* spp., *Galactia* spp., *Aletris lutea*, *Zigadenus* spp., *Polygala* spp., and *Xyris* spp. (Wharton 1978, Huck 1987, Platt et al. 1988b). Bridges and Orzell (1989) have documented the floristic relationships of west Gulf Coastal Plain longleaf pine communities. A common trait of shrubs and forbs of these pine forests is an underground storage organ (e.g., root crown, tap roots) that allows rapid regrowth of aboveground tissue following a fire (Hilmon 1968, Wharton 1978, Abrahamson 1984a,b, Platt et al. 1988b).

Pine flatwoods are subject to successional changes throughout their distribution. The accepted general pattern is that in the absence of recurring fires, hardwoods either already present in stands or invaders from adjacent source populations increase in abundance and gradually suppress the pines (Wells 1942, Wahlenberg 1946, Lemon 1949, Braun 1950, Quarterman and Keever 1962, Komarek 1974, Christensen 1981). Laessle (1942) produced a linear model of succession in flatwoods of north-central Florida. Based on field data from sites distributed across north-central Florida, Monk (1968) recognized the wide variation in pine flatwoods and hypothesized a more detailed successional model for the "flatwoods complex" (Fig. 4). The Laessle–Monk successional scheme demonstrated the potential of pine flatwoods to succeed toward a number of other community types dominated by hardwoods if fire were eliminated as an environmental factor. Soil moisture and climate limited the final expression of the vegetation.

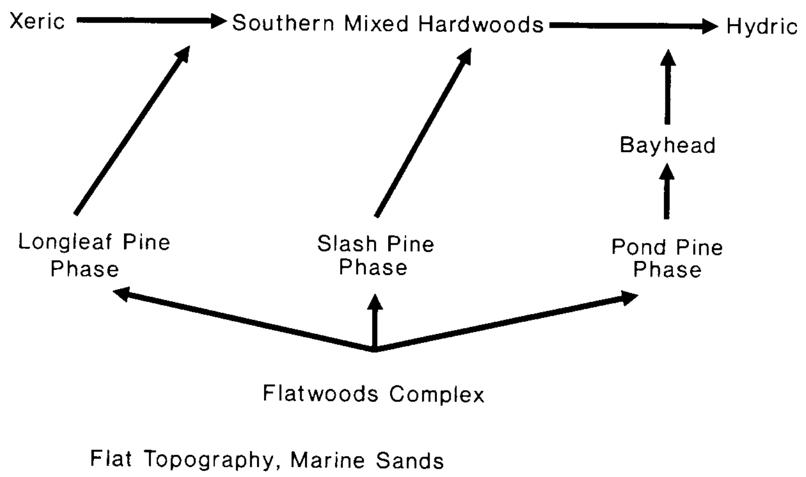

FIGURE 4. Model of succession in flatwoods. A lack of recurring fires in the longleaf and slash pine phases allows the pines to be replaced by hardwoods. Improved drainage allows the pond pine phase to progress to a bayhead. (Adapted from Monk 1968.)

Heyward (1939) documented hardwood invasion of a mixed stand of longleaf and slash pines that had been unburned for 12 years. His analysis of tree density by size class (DBH) clearly revealed the success of the hardwoods and the failure of the pines to reproduce. Laessle (1942) stated the absence of fire would lead to a loss of pines, increased soil moisture, and eventual loss of the relatively impermeable soil hardpan. These changes would set in motion the long-term trend toward a mesic hardwood forest. The major successional tendency observed by Quarterman and Keever (1962) was for pines to be replaced by hardwoods in Coastal Plain forests they examined from South Carolina to eastern Texas. In Florida, longleaf pine phase flatwoods tended to terminate in southern mixed hardwoods dominated by live oak (*Quercus virginiana*) (Monk 1965). Drier slash pine phases yielded mesic southern mixed hardwoods, whereas wetter slash pine and pond pine phases developed into bayheads. The conversion of an old-growth slash pine stand to a bay swamp was reported by Hebb and Clewell (1976).

Pine savannas and mixed pine–hardwood forests of east Texas were probably maintained by recurrent fires (Streng and Harcombe 1982, Schafale and Harcombe 1983, Bridges and Orzell 1989). Expansion of pineland and mixed forests into prairies has resulted from fire suppression (Schafale and Harcombe 1983). Expansion of pinelands in south Florida has resulted in their invasion of former wet and dry prairies (Richardson 1977). Although classical pine flatwoods do not occur in east Texas, longleaf pine stands in the Big Thicket have not undergone conversion to closed hardwood forests after 40 years of fire suppression (Marks and Harcombe 1981). Any conversion of longleaf pine forest to deciduous forest will take a much longer period although deciduous trees and shrubs are rapidly establishing.

Rockland Pinelands (Subtropical Pine Forest) Romans (1962) in the late 18th century described pinelands of extreme south Florida growing on limestone. Military and civilian explorers in the 19th century confirmed their existence in the vicinity of Miami, along Biscayne Bay, and on Long Pine Key (Olmsted et al. 1983). John Small studied the flora during the first 30 years of the 20th century. Harper (1927) referred to these forests as Miami Pine Land and associated them with Miami oolitic limestone. Classified by Küchler as subtropical pine forests (Fig. 1, Type 116 in southern Florida), we refer to them as rockland pinelands. Harper (1927) credited Small with having shown the understory shrubs and herbs of these pinelands to be unique in the high number of endemic and West Indian species. Davis (1943) mapped and described, apart from traditional pine flatwoods, the Miami rockland pine forest. The seminal work of Robertson (1955) first clarified in a systematic fashion the critical role of fire in the maintenance of the unique flora of rockland pinelands.

The Miami rock ridge and similar habitat settings in the Big Cypress Swamp west of the Everglades occupy the youngest geologic formations in North America. Florida south of Lake Okeechobee has been a relatively stable environment in terms of hydrology and climate for about the last 5000 years; however, sea-level rises (0.3 mm/yr) continue to be documented (Robbin 1984). Olmsted and Loope (1984) have suggested some form of pinelands may have been more widespread during the Wisconsin maximum; thus the present extent of pinelands may represent remnants of that former, more extensive distribution.

Davis (1943) provided an accurate map of the rockland pinelands based on aerial photos and field study and estimated the original area to have been 72,900 ha. The Miami ridge bordered the Everglades for some 80.4 km and varied in elevation from 6.1 m MSL near Miami to 0.45–0.61 m MSL at Mahogany Hammock in Everglades National Park. Disjunct stands of rockland pinelands occur west of the Everglades in the Big Cypress Swamp (Gunderson et al. 1982). Pinelands of the southeast coast occur on Miami Oolitic Limestone, whereas those of the Big Cypress are found on the highest bedrock outcrops of Tamiami Limestone (Craighead 1971, Gunderson and Loope 1982).

South Florida slash pine, *Pinus elliottii* var. *densa*, is the only species of pine found on the rockland soils. Rock ridges and islands experienced the shortest hydroperiods in the region, which are typically 1–2 months but may be up to 5 months (Gunderson et al. 1982). Height and diameter growth of this variety of slash pine occurs over a period of about 10 months (Langdon 1963). Hofstetter (1974) stated that these trees seldom ignite at the base when struck by lightning and may never carry a crown fire. Seedlings of this variety remain in the grass stage 2–5 years; smaller pines 2–6 m tall have a greater than 50% chance of surviving a hot ground fire.

Relatively few data exist on characteristics of existing rockland pineland; records from the former Miami rockland pinelands are nonexistent or unavailable. Second growth stands on Long Pine Key, Everglades National Park, supported from 453 to 1179 pines/ha with a range in basal area from 16.0 to 18.1 m^2/ha (Snyder 1986). Second growth stands of slash pine in the Turner River area, Big Cypress National Preserve, averaged 90 trees/ha with a basal area of 7 m^2/ha (Gunderson et al. 1982). Data on density and basal area of virgin stands of rockland pinelands in the preserve are not available (James R. Snyder, personal communication).

The understory vegetation of rockland pinelands is quite distinctive from pine flatwoods (Harper 1927, Davis 1943, Craighead 1971, Loope et al. 1979, Olmsted et al. 1983, Snyder 1986). Loope et al. (1979) recorded 186 native vascular plants and five exotics. Seventy-six of the 186 species were considered to be major elements of the community and 67 species were limited to or nearly limited to pinelands of south Florida. The rockland pinelands supported 32 of 65 plant taxa endemic to south Florida; furthermore, 17 of the 32 taxa were confined to the rockland pinelands. Among the pine forests of Florida, the rockland pinelands have the most endemics yet occupy the smallest area (Avery and Loope 1980).

The understory vegetation included many species of hardwoods, which tend to be tropical in origin (Olmsted et al. 1983). Examples of such woody species are *Dodonea viscosa*, *Guettarda elliptica*, *Psidium longipes*, *Bumelia salicifolia*, and *Myrsine floridana*. Temperate species also present are *Rhus copallina*, *Myrica cerifera*, *Ilex cassine*, *Persea borbonia*, and *Serenoa repens*. Olmsted et al. (1983) reported 95 taxa in the shrub stratum of south Florida pine forests. The diversity is rapidly reduced to the north as more freezes are encountered and the tropical elements drop out.

The ground-level vegetation is species rich and fire-adapted (Olmsted et al. 1983). Examples of these plants are *Dyschoriste oblongifolia* var. *augusta*, *Phyllanthus pentaphyllus* var. *floridanus*, and *Tragia saxicola*. Prominent grasses include *Schizachyrium rhizomatum* and *Andropogon cabanisii*. Woody plants, grasses, and herbs tended to flower within 4–16 weeks following a fire in March at Long Pine Key (Loope 1980).

Structure of rockland pinelands in the eastern portion of Big Cypress National Preserve is less complex than those of Long Pine Key. Fewer species of shrubs occur in the Big Cypress than on Long Pine Key (Olmsted et al. 1983). Typical understory plants associated with south Florida slash pine included saw palmetto, *Schizachyrium rhizomatum*, *Andropogon virginicus*, and *Paspalum monostachyum* (Gunderson and Loope 1982). Locally, *Serenoa* dominated slightly higher elevations, whereas the graminoids dominated lower areas (Gunderson et al. 1982).

Alexander and Crook (1974) outline successional pathways of pinelands of south Florida (Fig. 5). Recurrent fires result in pinelands dominated by *P. elliottii* on mesic sites over limestone or sand. High, dry sites of sand or sand and shell will support *P. clausa*. A lack of fire allows tropical and temperate hardwoods to develop and spread. Pine forests, if free of fire for several decades, come to be dominated by temperate (northward) hardwoods or tropical (southward) hardwoods. The time spans associated with these various successional stages are poorly documented (Duever 1984).

Literature reviewed by Alexander (1953) confirmed the historic presence of slash pine in the upper keys (e.g., on Key Largo) and in the lower keys (e.g., Big Pine, Little Pine, No Name, and Cudjoe). Loss or reduction of these pinelands occurred over a period of 200 years as tree harvesting and fire exclusion yielded successional trends favorable to tropical hammock formation. Alexander (1953) reported the replacement of slash pine on Key Largo by live oak and *Swietenia*

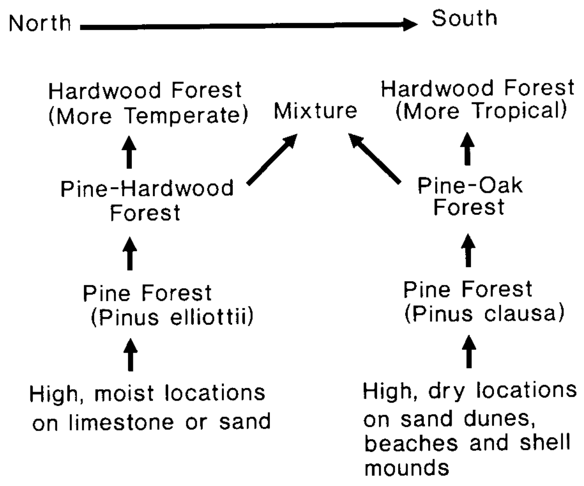

FIGURE 5. Model of succession in pinelands in south Florida to include the rockland pinelands, pine flatwoods, and sand pine scrub. (Adapted from Alexander and Crook 1974.)

mahagoni, with the latter species being replaced by another group of tropical hardwoods. In the lower keys, fire exclusion in pinelands of Big Pine Key was shown to be associated with a doubling in the number of slash pine over an 18-year period. Most of the increase was accounted for by pines under 3.6 m. Droughts and the construction of mosquito ditches complicated the isolation of fire exclusion as an explanation for these changes in the pine population structure and the composition and structure of the understory (Alexander and Dickson 1972). Nearby No Name Key showed a different response to fire exclusion and was heavily invaded by hammock species (Alexander and Crook 1974).

Longleaf Pine–Turkey Oak Sandhills The "High Pine Land" of Harper (1927) or "Sandhill Country" of Wells and Shunk (1931) is here named longleaf pine–turkey oak sandhills as used by Laessle (1942). Küchler (1964) did not map this widespread association. In contrast, Davis (1967) mapped the community as dominant over about 20% of Florida.

Geographic variation in the expression of longleaf pine–turkey oak sandhills has resulted in a plethora of names for the community type: high pine (Harper 1927), sandhill country (Wells and Shunk 1931), xerophytic deciduous forest, xerophytic coniferous forest (Pessin 1933), pine–turkey oak sandridge, fall-line sandhill, Florida sandhill association (Christensen 1986), clay ridge forest, dwarf oak forest, dwarf oak–evergreen shrub forest (Wharton 1978), turkey oak barrens, scrub oak barrens (Barry 1980), and sandhill pine forest (Marks and Harcombe 1981). Regardless of the local name, these communities occur on rolling topography with deep, well-drained sand, which is yellowish to cream-colored at the surface. Longleaf pine is the dominant tree throughout the range of the association with the exception of southeast and south-central Florida stands, which may have only slash pine or admixtures of the two species. Turkey oak (*Quercus laevis*) is a predictable subordinate tree within the association as far west as Louisiana (Table 4).

The distribution of the longleaf pine–turkey oak association is shown in Fig. 6. The association occurs in eastern Virginia on the Blackwater Ecological Preserve and south to Jupiter, Martin County, Florida. Marks and Harcombe (1981) report the community type in the "Big Thicket" region of southeast Texas. Interior stands occupy the fall line of Alabama, Georgia, North Carolina, and South Carolina (Wells 1924, Harper 1928, Wells and Shunk 1931, Weaver 1969, Wharton 1978, Barry 1980).

Analogues of the longleaf pine–turkey oak association may have been more widespread in the southeastern Coastal Plain since the late Pliocene. Efforts to reconstruct paleoenvironmental conditions from palynology and fossil records suggest the occurrence of savanna-like ecosystems over much of this region (Webb 1990). Increases in rainfall and elevated water tables within the last 5000 years (Watts 1975, 1980, Watts and Hansen 1988) may have resulted in a contraction of the association and other xeric pinelands.

Longleaf pine is a keystone species in the longleaf pine–turkey oak association. The life history of the species is replete with structural and physiological attributes that allow it to assume a dominant role in a landscape subject to frequent natural

TABLE 4 Composition of Pine–Oak Sandhill Communities of Florida, Georgia, and Texas

	Communities						
Species	Southern Florida[a]		Northeast Florida[b]		North Central Florida[c]	South Georgia[d]	Southeast Texas[e]
Pine							
Pinus clausa	3			3	19		
Pinus echinata							1.3
Pinus elliottii	24	5		12	50		
Pinus palustris			34	21	100	18	0.6
Pinus taeda					31		2.4
Oak							
Quercus chapmanii	2	10			19		
Quercus falcata					37		
Quercus geminata	18	10					
Quercus hemisphaerica			2				
Quercus incana			9	24	37	3	4.7
Quercus laevis	12		5	36	100	240	
Quercus margaretta					56	25	
Quercus marilandica					5		
Quercus myrtifolia	20	36	2		19		
Quercus stellata							3.7
Quercus virginiana			31	2	69		
Others							
Aristida stricta		2					
Carya floridana	12	9					
Carya glabra					19		
Cinnamomum camphora			1				
Cornus florida							0.1
Crataegus uniflora					25		
Diospyros virginiana			3		69	5	
Garberia heterophylla		3					
Ilex vomitoria							0.1
Licania michauxii		2					
Liquidambar styraciflua							0.1
Lyonia ferruginea	2						
Myrica cerifera			2		31		
Nyssa sylvatica					5		
Persea borbonia			1				
Prunus serotina			7		25		
Rhus copallina			3				
Sabal etonia	11	20					
Serenoa repens	1	3					
Vaccinium stamineum							

[a] Percent cover >1%; Archbold Biological Station (Abrahamson et al. 1984).

[b] Percent density (Veno 1976).

[c] Tree frequency; 16 sites of north-central Florida (Monk 1968).

[d] Importance values (relative density + relative frequency + relative dominance); two Georgia sites (Faust 1976).

[e] Basal area (m^2/ha) for two east Texas sites (Marks and Harcombe 1981).

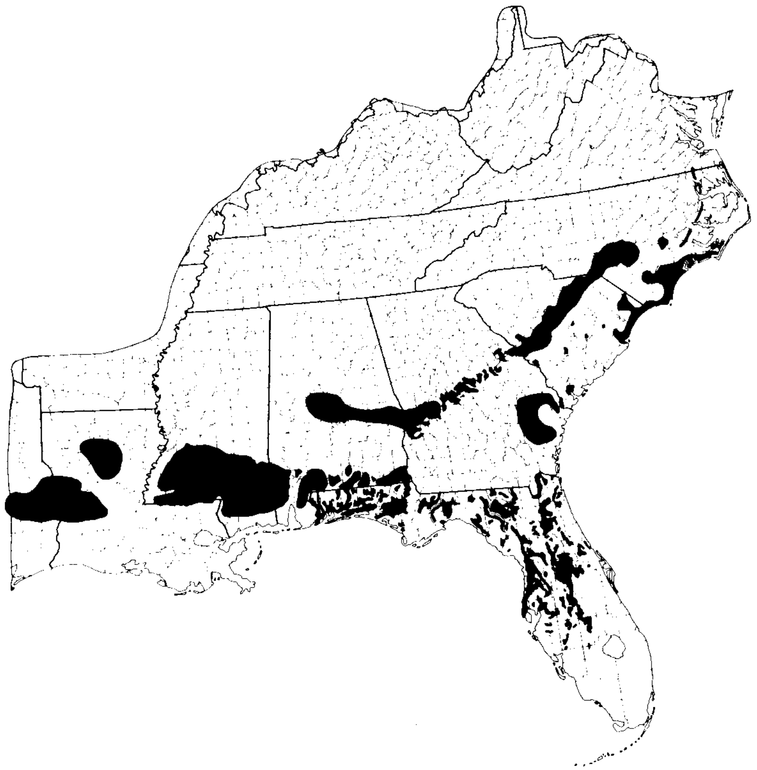

FIGURE 6. Distribution of the longleaf pine-turkey oak sandhill association in the southeastern U.S. Smaller but significant examples of the association occur in the lower Coastal Plain of South Carolina, Georgia, and in central and south Florida but are not indicated on the map. Turkey oak is not found west of extreme eastern Louisiana and is replaced by other oaks such as blue-jack (*Q. incana*) in the western examples of the sandhill community. The distribution in Florida is after Davis (1967).

fires (Wahlenberg 1946, Fowells 1965, Platt et al. 1988a). Germination occurs in the fall after seeds have reached openings with mineral soil exposed. Initially, aboveground growth is largely confined to needle production and formation of the "grass stage," which may persist 3–7 years or longer. Tap root growth continues until a relatively constant source of groundwater is reached. During the grass stage, pine seedlings readily survive "cool" ground fires. Seedlings are vulnerable to fire during initial growth up to heights of 0.9–4.5 m. Thereafter, longleaf pine, insulated by its thick bark, is seldom killed by fire.

Longleaf pine–turkey oak sandhill association was recognized by Laessle (1942, 1958a) as a "fire climax." Fires at intervals of 1–3 years were claimed to be responsible for the park-like (savanna) appearance in which individual longleaf pine over 30 m tall stood over a dense ground layer of wiregrass and other herbaceous elements (Wells and Shunk 1931, Parrott 1967). Casting of pyrogenic needles in early spring by longleaf pine provides a dry fuel to be ignited by a lightning strike during late spring or early summer (Platt et al. 1988a). Wiregrass assumes a keystone role along with longleaf pine in that its foliage carries the ground fire.

The structure and composition of this association is predictably variable owing to its broad geographic range (Fig. 6). Phases of the association have been designated in many cases. A pioneer study by Wells and Shunk (1931) named three phases of *Pinus palustris–Aristida stricta* stands, each identified with a different midstory tree: (1) turkey oak, (2) bluejack oak (*Quercus incana*), and (3) mockernut hickory (*Carya tomentosa*). These forests were derived from a fire-maintained community composed of longleaf pine, dogwood (*Cornus florida*), and wiregrass. These old-growth stands of longleaf pine were quickly clearcut as the Coastal Plain was settled. Pessin (1933) described this association in the Gulf Coastal Plain of Alabama, Mississippi, and extreme eastern Louisiana, where harvesting of longleaf pine had released the midstory oaks such as turkey oak (ridge tops) and blackjack oak (*Q. marilandica*) (well-drained flatwoods). A similar pattern was noted by Laessle (1942) at Welaka, Florida, with longleaf pine and turkey oak on higher elevations and bluejack oak replacing turkey oak at slightly lower elevations. These pioneer studies of the association and its variation in space revealed in a qualitative way the combined impacts of earlier harvesting of pine and the trend to suppress fires in xeric pinelands in general. These two acts led to a shift in singular pine dominance to pine–oak codominance.

Monk (1968) sampled 16 stands of the longleaf pine–turkey oak association in a six-county area representing the major sandhill systems of north and central peninsular Florida. His stands included 19 tree species; only the dominants occurred in all stands (Table 4, area 3). Three phases of the association were recognized: (1) turkey oak phase on the most xeric, sterile sites, (2) southern red oak (*Q. falcata*) phase over limestone deposits, and (3) sand post oak (*Q. margaretta*) phase over soils with nutrient availability intermediate to phases 1 and 2.

Faust (1976) sampled two communities of the longleaf pine–turkey oak in the Georgia fall-line sandhills (Table 4, area 4). The tree data reflected the dominance of oaks and particularly turkey oak over the heavily harvested longleaf pine. Dominant shrubs included *Asimina parviflora*, *Cornus florida*, *Crataegus flava*, and *C. uniflora*. Prominent herbaceous genera included *Aristida*, *Andropogon*, *Panicum*, *Erigeron*, *Krigia*, and *Liatris*. Additional plant compositional data from fall-line sandhills were given in Duke (1961) and Bozeman (1971).

A resurvey of Laessle's (1958b) sandhill quadrats by Veno (1976) revealed further local variation in the expression of the association (Table 4, area 3, columns 3 and 4). One site was treated as representative of the bluejack oak phase while a second was of the turkey oak phase. Live oak was very prominent (IV = 170) in the bluejack oak phase. Veno (1976) suggested a live oak phase in a successional scheme for these xeric pinelands.

Sandhill communities once covered most of the southern Lake Wales Ridge of south-central Florida (Laessle 1958a, Davis 1967, Abrahamson et al. 1984). Slash pine dominates present-day stands; however, longleaf pine may also be found in these stands. Detailed studies on remnants of these communities at the Archbold Biological Station by Abrahamson et al. (1984) suggested two phases within the association: (1) turkey oak and (2) scrub hickory (*Carya floridana*). The turkey oak phase occurred at higher elevations on well-drained soils, whereas the hickory phase was on lower elevation sites on somewhat less well drained soils (Table 4, area 1, columns 1 and 2).

The western limit of the longleaf pine sandhill community is in the "Big Thicket" region of southeast Texas (Marks and Harcombe 1981). Marks and Harcombe (1981) described sandhill pine forest as occurring on river terraces with little relief and deep, sandy soils. Longleaf pine was widely scattered with bluejack oak and post-oak (*Q. stellata*) having much more basal area than the pines. These two oaks replace turkey oak in the sandhill community west of the Mississippi River (Table 4, area 5). Bridges and Orzell (1989) summarized knowledge on longleaf pine savannas in eastern Texas and Louisiana.

Hardin and White (1989) reviewed the rare vascular plants found in association with wiregrass and listed 191 rare taxa. Based on The Nature Conservancy's Heritage Program Methodology, 122 taxa were considered to be threatened or endangered throughout their ranges.

Successional dynamics and fire are inexorably linked in the longleaf pine–turkey oak sandhill community (Laessle 1942, 1958a, Monk 1968, Davis 1985, Myers 1985, Myers and White 1987, Platt et al. 1988b, Rebertus et al. 1989). Laessle (1942) hypothesized a linear successional model for the community such that an absence of fire would result in Clementsian convergence of stands to a regional climatic climax dominated by *Magnolia* and *Ilex*. Harper (1927) observed that in prehistoric times fires could run for miles through the "high pine" and that it was likely every spot must have burned every year or every second year. In coastal North Carolina, Wells and Shunk (1931) recognized that wiregrass presence in the ground layer significantly favored the pyrogenic nature of the community. Chapman (1932) recognized longleaf pine as a dominant in fire climax stands with various grasses (wiregrass, *Andropogon* spp., and *Muhlenbergia* sp.). Elaboration of the Laessle model of succession by Monk (1968) showed that local site conditions within the range of the community yielded three phases of which the most common was characterized by turkey oak. Elsewhere, Veno (1976) suggested two additional phases and Abrahamson et al. (1984) added another (Fig. 7). It was assumed these phases would persist as long as annual or biannual fires reached them. They will persist, at least in some cases, with considerably longer fire frequency.

Longleaf pine–turkey oak habitat islands within the Ocala National Forest may have persisted at elevations above 30 m MSL since before the Pleistocene (Kalisz and Stone 1984a). However, boundaries of the habitat islands have not been stable with respect to adjacent sand pine scrubs as biogenic opal extracted from their soils showed inconsistencies in mass and morphology. Kalisz and Stone (1984a) interpreted their results to mean that variation (shifts) in boundary conditions due to changes in fire regimes allowed sand pine scrub to invade former longleaf pine–turkey oak stands, and, to a lesser extent, longleaf pine to invade scrub. Nonetheless, at the landscape level recurrent fire explains community persistence and spatial distribution.

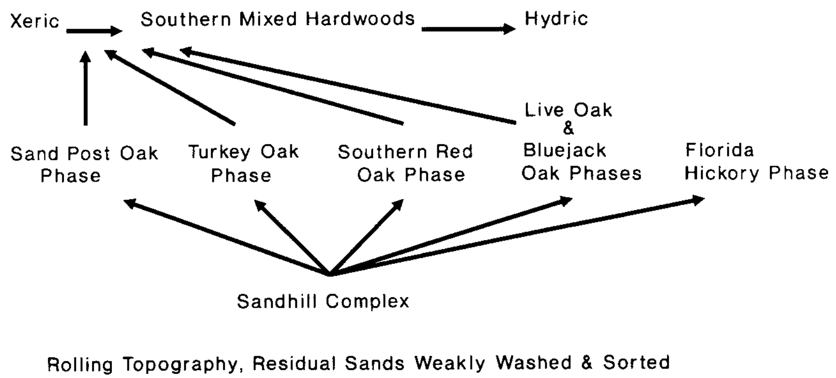

FIGURE 7. Model of succession in sandhills of Florida based on elimination of recurring fires and various phases of the community type progressing toward hardwood domination. (Adapted from Monk 1968, Veno 1976, and Abrahamson et al. 1984.)

A lack of recurrent fires in longleaf pine–turkey oak sandhills should result in succession toward a xeric hammock (Fig. 6). Laessle (1958b) established permanent quadrats in 1951 on the Welaka area he had studied earlier (Laessle 1942). With respect to the site in longleaf pine–turkey oak, only sand pine (*Pinus clausa*) had invaded in the intervening 20 years. He also surveyed the adjacent sandhill community and found some invasion of fire-intolerant trees. Veno (1976) resurveyed Laessle's plots after 40 years of fire suppression and found further evidence of mesic tree invasion, for example, American holly (*Ilex opaca*) and southern magnolia (*Magnolia grandiflora*). Myers and White (1987) examined the longleaf pine–turkey oak plot described by Laessle (1958b) and Veno (1976). They found fewer individual sandhill species and a noticeable invasion of scrub and mesic species. Sand pine was a notable invading species. These studies offered conclusive evidence that fire suppression leads to important changes in the species composition of longleaf pine–turkey oak sandhill communities.

Givens et al. (1984) analyzed permanent plots in a southern ridge sandhill at the Archbold Biological Station. Their data reflected changes due to self-thinning and some shifts in species composition, but clear trends in succession were not evident in the 10-year study period. Several decades of observation may be necessary to demonstrate successional trends (Veno 1976, Myers and White 1987).

Myers (1985) studied an undisturbed ecotone between sand pine scrub and southern ridge sandhill at the Archbold Biological Station. Several types of evidence, including historic photographs, soil profile changes, and pine age structures showed that the sandhill stand had been invaded by scrub species. Furthermore, the present trend was toward a xeric hardwood forest. A successional model to describe these findings was proposed (Fig. 8). Tests of the model (Myers and White 1987) suggested site-specific patterns of succession were influenced by past

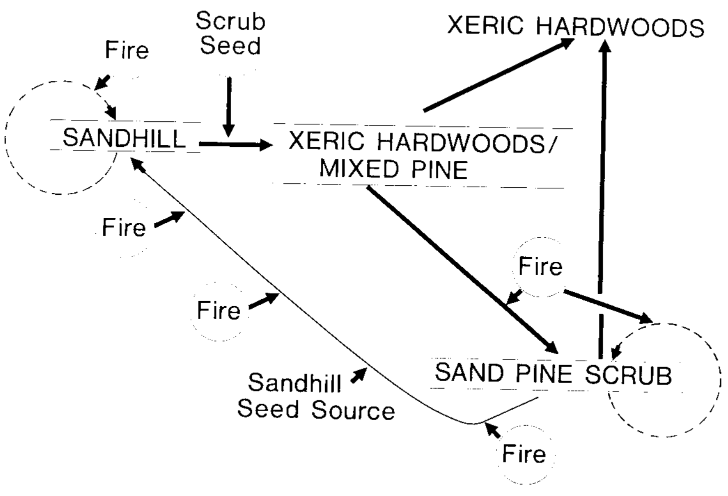

FIGURE 8. Model of successional pathways that may be followed over several hundred years with alternating fire frequencies and dominance by pine and oak species shifting temporally. (Adapted from Myers 1985.)

land-use history, fire regimes, and edaphic factors. Indeed, Peroni and Abrahamson (1986) concluded that southern ridge sandhills in Highlands County, Florida, have undergone little change in species composition over the last half-century. Rather, woody vegetation has increased in stature while understory and ground cover vegetation have been reduced. These changes were linked to a reduction in fire frequencies.

Successional studies in longleaf pine–turkey oak vegetation outside Florida are rare. Bozeman (1971) completed a detailed study of sand ridge vegetation in the Coastal Plain of Georgia. When released from fire, these communities succeeded to a xeric hammock dominated by laurel oak (*Quercus laurifolia*).

Sand Pine Scrub (Küchler Type 115) Sand pine scrub is limited to Florida and coastal dunes in Alabama as far west as Mobile Bay (Fig. 1; central Florida). A single stand has been discovered in Mississippi (D. R. Richardson, personal communication). Typically, this community is characterized by a tree layer of sand pine and a dense understory of evergreen shrubs. Webb (1990) states that a two-needle pine (sand pine?) was far more widespread in the northern half of Florida in the Late Pleistocene. Analogues of modern scrub probably reached their maximum areal extent during the Wisconsin full glacier stage (Watts 1975, Webb 1990). The most extensive example of this community is the land encompassed by the Ocala National Forest in north-central Florida (84,987 ha). Most remaining examples of the community range in area from 40.4 to 242 ha and occur as an archipelago of habitat islands that may be correlated with Miocene, Plio-Pleistocene, or Pleistocene shorelines (Laessle 1968). Wharton (1978) described three communities in Georgia—dwarf oak-evergreen shrub forest, evergreen scrub forest, and evergreen scrub-lichen forest—that could be treated as variations of sand pine scrub, albeit without sand pine in the modern flora.

Sand pine is normally restricted to sandy, acidic, excessively drained, nutrient-deficient soils of marine origin. This also describes the edaphic features of typical scrub habitat. Soils where scrubs and sand pine occur along the Gulf coast of Florida and Alabama are white and often referred to as sugar sand. In contrast, soil in the Ocala National Forest was derived from the Citronelle geological formation and is buffy yellow at the surface. Southward in the peninsula scrubs most often occupy St. Lucie soil, which is white; however, yellow sands also may support sand pine and its scrub associates (Christman and Judd 1990, I. J. Stout, personal observation).

The disjunct distribution of sand pine is loosely correlated with variation in serotiny. Western populations of the species are commonly referenced as the Choctawhatchee race, characterized as nonserotinous and observed in uneven-aged stands (Fowells 1965). Typical populations of the peninsular or Ocala race are serotinous and occur in dense, even-aged stands of pyrogenic origin. Sand pine elsewhere in peninsular Florida varies within stands as to the proportion of individuals with closed cones (Latham 1985, Myers and White 1987, I. J. Stout, personal observation). This variation in the serotiny results in stands with uneven age distributions and allows sand pine to invade adjacent sandhill sites in the absence of fires (Givens et al. 1984, Myers 1985, Myers and White 1987). In the absence of fire, sand pine develops heart rot (Ross 1973), and wind throw is a common cause of mortality. Individuals older than 70 years are rare in mainland populations, whereas barrier island populations may be much older; individuals of sand pine on Dog Island were estimated to be 125 years old (Anderson and Alexander 1985).

The structure of sand pine scrub communities varies as they recover following disturbance by fire or harvesting. In pyrogenic stands ranging from 20 to 40 years postdisturbance, sand pine dominated in basal area and density (Lugo and Zucca 1983, Latham 1985) (Table 5). Laessle (1965) demonstrated that dispersion patterns in pyrogenic stands of sand pine changed with stand age from random or aggregated (<23 years) spacing to regular spacing (>23 years). A 12-year-old stand had a stem density of 25,700/ha and was randomly dispersed, whereas a 66-year-old stand was regularly dispersed with a stem density of 370/ha.

Evergreen sclerophyllous shrubs dominate the understory in sand pine scrub (Table 6). Most prominent are oaks, *Quercus myrtifolia*, *Q. geminata*, and *Q. chapmanii; Q. inopina* may be locally abundant within scrubs of the Lake Wales Ridge region (Johnson and Abrahamson 1982). Latham (1985) recorded 32 species in the shrub layer of 20 sample sites in central Florida. Species with high constancy included *Serenoa repens*, *Lyonia ferruginea*, and *Ceratiola ericoides*. Scrubs of the Lake Wales Ridge typically include *Carya floridana* and *Sabal etonia* (Abrahamson et al. 1984). Woody stem densities of scrubs may be quite high and individual stands appear impenetrable (Latham 1985). Lugo and Zucca (1983) reported 33,316 woody stems/ha from a stand in the Ocala National Forest.

TABLE 5 Overstory of Sand Pine Scrub Communities of Central and North Florida[a]

Species	Density (No./ha) (1)	Density (No./ha) (2)	Frequency (%) (1)	Frequency (%) (2)	Basal Area (m^2/ha) (1)	Basal Area (m^2/ha) (2)
Pinus clausa	672	717	69	42	25.26	10.62
Quercus geminata	139	18	29	3	0.56	0.02
Lyonia ferruginea	237	18	33	3	0.58	0.01
Quercus myrtifolia	233	251	27	18	0.67	0.38
Quercus chapmanii	156	35	27	6	0.66	0.08
Carya floridana	13	—	2	—	0.03	—
Quercus laevis	6	179	1	27	0.07	0.82

Source. (1) Adapted from Latham (1985); (2) adapted from Lugo and Zucca (1983).

[a] Plants ≥2.5 cm DBH.

Many shrub species in sand pine scrub undergo vegetative reproduction as opposed to seeding following a fire. Oak species, *Serenoa* and *Sabal etonia*, recover rapidly (Abrahamson 1984b). Another subset of species recover from fires by seedling establishment: *Ceratiola ericoides*, *Dicerandra* sp., *Calamintha ashei*, and *Conradina brevifolia*. Of these obligate seeders, *Ceratiola* has been studied in detail (Johnson 1982, Johnson et al. 1986). Sprouter species have an initial advantage over seeders and recover quickly following a fire; however, after about 30 years the biomass of *Ceratiola* was roughly equal to that of *Quercus inopina*, a sprouter (Johnson et al. 1986).

Ground-layer vegetation in sand pine scrub is sparse and species poor. Open sandy areas may alternate with dense stands of lichens (*Cladonia* spp.), *Selaginella arenicola*, and, more rarely, *Leucobryum albidum*. Herbaceous elements include *Chapmannia floridana*, *Panicum patentifolium*, *Dicerandra frutescens*, *Eryngium cuneifolium*, *Calamintha ashei*, *Liatris ohlingerae*, *Paronychia chartacea*, and *Rhynchospora megalocarpa* (Abrahamson et al. 1984, Latham 1985).

Age and isolation of sand pine scrub habitat islands have contributed to significant endemism among scrub-plant taxa (Ward 1979, Judd and Hall 1984, Christman and Judd 1990). The greatest density of endemic plants was found in the sand pine scrubs of the Lake Wales Ridge (Ward 1979, Christman and Judd 1990). Autecologic studies have further defined the role of disturbance in the life history evolution of these species (Johnson 1982, Putz and Minno 1987, Hartnett and Richardson 1989). Hartnett and Richardson (1989) found the endemic scrub morninglory (*Bonamia grandiflora*) responds to fire by recruiting from a seed bank and by increased clonal stem production.

Harper (1927) observed that fire destroys sand pine scrub, but that sand pine cones open to reseed the species and that the shrubs merely resprout from existing roots. It was implicit in Harper's writing that recovery followed disturbance rather than succession. Recent studies (Abrahamson 1984a, Latham 1985) have recognized this pattern to follow the initial floristics model of succession as proposed by Egler (1954).

TABLE 6 Understory Composition of Sand Pine Scrub Communities from South, Central, and North Florida

Species	South Florida[a] (1)	South Florida[a] (2)	Central and North Florida[b] (3)	Central and North Florida[b] (4)
Pine				
Pinus clausa	75	5	—	—
Oak				
Quercus chapmanii	7	1	1743	1469
Quercus geminata	8	—	2050	2939
Quercus inopina	—	7	351	—
Quercus myrtifolia	24	—	8423	22053
Others				
Carya floridana	20	—	68	—
Ceratiola ericoides	—	55	936	979
Conradina grandiflora	—	—	—	979
Garberia heterophylla	—	—	112	—
Gaylussacia frondosa	—	—	221	—
Lyonia fruticosa	—	—	—	1469
Lyonia lucida	—	—	459	—
Lyonia ferruginea	20	—	1734	—
Osmanthus americana	—	—	197	—
Palafoxia feayi	—	—	88	—
Persea borbonia var. humilis	—	—	167	—
Sabal etonia	26	1	2449	—
Serenoa repens	16	2	3469	—
Vaccinium myrsinites	—	—	166	979
Vaccinium stamineum	—	—	494	—
Vitis rotundifolia	10	—	—	—

[a] Percent cover >2%; (1) oak phase, (2) rosemary phase; Archbold Biological Station, Florida (Abrahamson et al. 1984).

[b] Density (No./ha); woody plants <2.5 cm DBH; adapted from Latham (1985) (3) and Lugo and Zucca (1983) (4).

Harper (1927) and earlier writers reviewed by Mulvania (1931) claimed no relationship existed between sand pine scrub and "high pine" (= longleaf pine–turkey oak association) in that taxa from neither community appeared to invade the other. (See discussion in section on sandhills.)

Mechanisms for the maintenance of local boundaries between sand pine scrub and longleaf pine–turkey oak stands may involve allelopathic effects alone or coupled with other factors. Richardson and Williamson (1988) demonstrated that aqueous leachates from the foliage of scrub plants inhibited reproduction and growth of grasses characteristic of sandhill communities. Shrubby species such as *Conradina canescens* and *Calamintha ashei* may chemically inhibit fire-prone grasses and thereby maintain the scrub and its boundaries (Williamson et al. 1989; D. R. Richardson, personal communication).

Laessle (1942) and Monk (1968) diagrammed succession of sand pine scrub to xeric hammock in the absence of fire (Fig. 9). Laessle (1942, 1958a) claimed that an absence of fire would allow oak domination over sand pine and the eventual formation of a xeric hammock (= forest dominated by broadleaf evergreen trees). Much of Laessle's argument hinged on the lack of sand pine regeneration in the absence of fire and the species' relatively short life span (70–100 years). The Bear Point scrub (Highlands County, FL) was claimed by Laessle (1968) to have succeeded to a xeric hammock. Peroni and Abrahamson (1986) suggested a "hickory phase" southern ridge sandhill community may have been the antecedent stage for this stand. Isolated sand pine scrubs may lose their sand pine if fires recur before cone-bearing individuals are present. Peroni and Abrahamson (1986) cited two instances that may fit this pattern; both stands were classified as scrubby flatwoods.

The lack of ground cover in the "rosemary" phase sand pine scrub may preclude fire as a regularly recurring disturbance. Nonetheless, in natural landscapes, oak phase sand pine scrub or scrubby flatwoods interdigitates with the rosemary phase; fires in these communities occasionally reach and burn the rosemary phase (Johnson and Abrahamson 1990). Rare or absent herbaceous taxa usually reappear in the understory following these fire events.

Successional patterns of coastal sand pine scrubs have been discussed by Richardson (1977) and Austin et al. (1987). Richardson (1977) recognized alternative paths for successional change in scrubs with different histories of erosion that were now associated with an increased frequency of fire. A decline in the number of species of herbaceous taxa with time since the last disturbance of coastal scrubs was reported by Austin et al. (1987). In contrast, on the southern Lake Wales Ridge, Givens et al. (1984) noted little change in species composition after 10 years, but shade-intolerant herbs (e.g., *Balduina augustifolia* and *Lechea deckertii*) were lost from permanent plots.

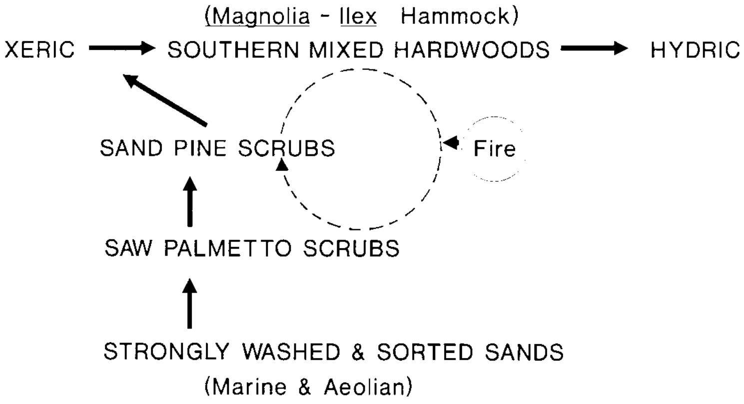

FIGURE 9. Model of succession in sand pine scrub with and without recurring fires. In the absence of fire, sand pine scrub converges with southern mixed hardwoods on the drier end of the soil-moisture gradient (Laessle 1942, Monk 1968).

Scrubby Flatwoods The first known reference in the ecological literature to scrubby flatwoods was by Laessle (1942) in his discussion of the Welaka Area, northeast Florida. The very name scrubby flatwoods implied a transitional community. However, Laessle (1942) treated it as an association under the heading "Scrub" with sand pine scrub as the primary association. In his monograph on the xeric pinelands of Florida (Laessle 1958a), he does not mention scrubby flatwoods. Monk (1968 and subsequent papers on Florida vegetation) does not mention scrubby flatwoods as a community type. Stout et al. (1976) recognized the community on Merritt Island off Florida's east coast. Richardson (1977) offered no historic record of the association but treated scrubby flatwoods as a "subdivision" under pine flatwoods. An endemic oak, *Quercus inopina*, was identified with scrubby flatwoods of the southern Lake Wales Ridge by Johnson and Abrahamson (1982). Laessle (1942) reported that scrubby flatwoods were characterized by a dense shrub layer of *Quercus geminata*, *Q. myrtifolia*, and *Q. chapmanii*. Significantly, wiregrass was present in the ground layer, whereas it was absent or extremely rare in sand pine scrub. Other scrub species such as sand pine, *Osmanthus americanus*, holly, and *Persea borbonia* var. *humilis* were missing.

In general, recent descriptions support those by Laessle. Scrubby flatwoods are dominated by evergreen, sclerophyllous shrubs. Woody stem densities are far less in scrubby flatwoods than in sand pine scrub. More open space between individual shrubs and the presence of wiregrass and other herbaceous elements in these openings also distinguish scrubby flatwoods from sand pine scrub (Abrahamson et al. 1984).

The distribution of scrubby flatwoods is apparently within the geographic limits of sand pine scrub, with which it is easily confused and the community type has not been mapped. It appears to be more fundamentally tied with scrub than with flatwoods as pine flatwoods extend far to the north and west along the Atlantic and Gulf Coastal Plain where scrubby flatwoods have not been reported. Scrubby flatwoods appear to be related to elevated local relief within flatwoods, which often grades upslope into sand pine scrub (Laessle 1942). The water table is therefore, 0.9–1.2 m below the surface and may be associated with a spodic layer. Nonetheless, drainage is substantially better than in flatwoods.

Abrahamson (1984a,b) reported on observations and experiments carried out to understand the role of fire in scrubby flatwoods. Generally, the fires must occur under special meteorological conditions (low humidity and high winds) to burn the community. Species such as *Quercus inopina* and *Q. geminata* recovered rapidly following fire and aboveground cover was at preburn levels within 2–3 years (Abrahamson 1984b). The natural burn cycle is not documented for the association, but Abrahamson (1984a) suggested scrubby flatwoods burned more frequently than sand pine scrubs. As in the case with sand pine scrub, fire is not a succession-initiating disturbance in scrubby flatwoods where most species resprout. Givens et al. (1984) reported no successional changes and only minor structural modifications on permanent plots in scrubby flatwoods after 10 years. Using a broader landscape approach, Peroni and Abrahamson (1986) corroborated the findings of Givens et al. (1984).

Successional Plant Communities

All pinelands of the southeastern Atlantic and Gulf Coastal Plain are successional in the absence of recurring fires. Fire frequency, soil moisture, and elevation largely explain local variation in and dominance by the various pine species. Closely associated with pinelands is a mix of wetland and upland communities either antecedent to or derived from pinelands (Table 7). Examples of these communities from peninsular Florida illustrate the landscape mosaic and successional interactions that may be anticipated. Early observers of pinelands recognized seral stages and some general patterns of change but did not fully appreciate the significance of fire in the vegetation dynamics (e.g., Gano 1917, Pessin 1933). Laessle (1942) and Monk (1968) called attention to most of the successional patterns implied in Table 7.

Documentation of these predictions from repeated measurements on permanent plots comes from Veno (1976) and Hartnett and Krofka (1989). Givens et al. (1984) showed that long-unburned pinelands in general change very little over a period of one decade. Fragmentation of habitats and the corresponding loss of nearby seed sources may reduce or eliminate potential species replacement patterns. Experimental fires as employed by Abrahamson (1984a), Hartnett (1987), Platt et al. (1988b), and Rebertus et al. (1989) examined individual species' response to disturbance to better understand community-wide responses. Long-term observations on permanent plots offer the best opportunity to understand disturbance–response dynamics in the context of natural area management in the future.

ANIMAL COMMUNITIES

The mobility of animals makes the definition of animal communities more arbitrary than in the case of plants. Mechanistically, communities may be defined based on species lists derived from point samples and analyzed statistically (e.g., by cluster analysis). Alternatively, assemblages may be defined along taxonomic lines (e.g., birds) and ignore other elements. The approach taken here is to assemble listings of species typically reported from habitats that represent particular plant associations. Because hundreds of species comprise the fauna of the pinelands of the Coastal Plain, only a few species are listed or discussed. An even smaller subset of the fauna could be considered limited in distribution to one of these habitat types. Thus omission of a species from a particular habitat type does not imply that it may never occur there.

TABLE 7 Summary Matrix of Successional Relationships Between and Among Communities of Pinelands of the Southeastern Coastal Plain

	Swale	Cypress Dome	Bayhead	Pond Pine Forest	Pine Flatwoods	Scrubby Flatwoods	Sandhill	Sand Pine Scrub	Xeric Hammock
Swale	Fire[a] Topography	—[c]	—	—	—	—	—	—	—
Cypress dome	Seral[b]	Saturated soils[d] Topography	—	—	—	—	—	—	—
Bayhead	Seral[b]	Seral[b]	Saturated soils[d] Topography	Seral[b]	Seral[b]	—	—	—	—
Pond pine forest	Seral[b]	—	—	Fire[a] Soils[d]	—	—	—	—	—
Pine flatwoods	—	—	—	—	Fire[a]	—	—	—	—
Scrubby flatwoods	—	—	—	—	—	Fire[a]	—	—	—
Sandhill	—	—	—	—	—	—	Fire[a]	Seral[b]	—
Sand pine scrub	—	—	—	—	—	—	Seral[b]	Fire[a]	—
Xeric hammock	—	—	—	—	—[b]	—[b]	—[b]	—[b]	Climate[e]

Note. Major habitat features (e.g., saturated soils) are noted if critical to successional development; minor successional pathways are not shown.

[a] Recurrent fires maintain the community.

[b] Succession of column community into row community.

[c] No known relationship between existing and stable type.

[d] Edaphic control of stable type.

[e] Climatic control of stable type.

Regional Richness

The biogeographic origins of animals in the southeastern Coastal Plain are highly variable depending on the groups being considered (Burleigh 1958, Mount 1975, Dundee and Rossman 1989). For instance, some invertebrates and many of the birds exhibit tropical affinities (Neill 1957), while most of the terrestrial mammals came from the north and west (Lundelius et al. 1983) with little exchange with the West Indies.

Relative to other states and regions, species richness is high for herpetofauna, 134 and 132 species in Alabama and Florida, respectively (Mount 1975, Dalrymple 1988), but low for breeding terrestrial birds and mammals (Kiester 1971, Layne 1974b). Amphibians and reptiles are presumably abundant because of the warm temperate climate, numerous river systems, and the presence of many wetlands in the region. More difficult to explain is the faunal impoverishment of birds and mammals in the southeastern Coastal Plain (Robertson and Kushlan 1974). The peninsular effect, as described by Simpson (1964) and MacArthur and Wilson (1967), provides a partial explanation for this phenomenon (particularly for the Florida peninsula) but does not completely explain the paucity of birds throughout the southeastern Coastal Plain (Robertson 1955, Cook 1969, Rohwer and Woolfenden 1969, and Tramer 1974). Robertson and Kushlan (1974) concluded that the explanation of this region-wide paucity of birds lies in several poorly understood biogeographic phenomena. The peninsular effect with respect to Florida's herpetofauna may be explained by habitat reduction alone (Means and Simberloff 1987).

In marked contrast to the depauperate situation with breeding birds and mammals in the southeastern Coastal Plain, this region (and especially Florida) serves as an important migratory funnel and corridor for birds that winter in the West Indies and South America. Thus dramatic differences are obvious in bird use of pineland habitats and in avian species richness due to this influx of migrants and winter residents. Northbound migrants in good weather may cross the Coastal Plain and fly directly to the Piedmont, however. Hamel et al. (1982) have presented very useful documentation of year-round avian use of these forested habitats.

Another characteristic of the biota of this region is a relatively high incidence of endemism resulting in some very specialized plants and animals. However, many nonendemic species are also very specialized. The relatively high incidence of threatened and endangered species in the region is partially explained by endemism (Cooper et al. 1977, McDiarmid 1979, Ward 1979).

Community Assemblages

Pine Flatwoods Collectively, a rich fauna is associated with the widespread pine flatwoods community. For example, Layne (1974a) reported 87 species of vertebrates in his study area of slash and longleaf pine in north-central Florida. Part of this diversity is explained by the pronounced interdigitation of pine flatwoods with other community types (e.g., cypress domes and strands, bottomland hardwoods, and a variety of herbaceous wetlands). Habitat shifts by various faunal elements may be observed on a daily, seasonal, and annual basis.

Characteristic Animals Invertebrates of pine flatwoods are as a group poorly studied. Table 8 lists some common species of the pine flatwoods. Conspicuous insects associated with saw palmetto include walking sticks (Phasmatids), a beetle (*Hemisphaerota cyanea*), and paper wasps (Polistids). Whitford and Gentry (1981) studied the ant communities of longleaf pine plantations in South Carolina. Four species of ants were found to dominate all pine plantations: *Crematogaster lineolata*, *Aphaenogaster traetae*, *A. fulva*, and *Conomyrma insana*. Termites (*Reticulitermes flavipes* and *R. virginicus*) were associated with dead wood in the pine plantations (Gentry and Whitford 1982). Arachnids of note included chiggers (*Trombicula* spp.) and ticks such as *Dermacentor variabilis*, *Amblyomma americanum*, and *Ixodes* spp. The most common ground surface spiders reported by Corey and Taylor (1988) were *Hahnia cinerea*, *Sosippus floridanus*, and *Habrocestum bufoides*. The most frequently sampled foliage spiders were *Hentzia palmarum*, *Peucetai viraidans*, and *Misumenops celer* (Corey and Taylor 1989). The centipede *Neolithobius xenopus* and the millipede *Dicellarius okefenokensis* were reported from longleaf pine flatwoods of central Florida (Corey 1988).

Characteristic amphibians and reptiles of pine flatwoods are listed in Table 9. Study of cypress ponds embedded in pine flatwoods of north Florida revealed 20 species of reptiles and 18 species of amphibians (Vickers et al. 1985). Sixteen of the 38 species were considered to be aquatic with the remainder spending portions of their life cycles in the surrounding flatwoods. Enge and Marion (1986) reported an average of 22.8 species per drift-fence array ($n = 4$) in a naturally regenerated 40-year-old stand of *Pinus elliottii* in north Florida. The dominant species among the 36 captured was the spadefoot toad ($n = 4722$). Mount (1975) stated the flatwoods salamander was nearly extirpated from Alabama because of drainage. The eastern indigo snake was sighted in pine flatwoods of Georgia on one occasion ($n = 68$) (Diemer and Speake 1988); whereas in Florida its occurrence in flatwoods was not unusual (Moler 1985).

Bird communities of southeastern pinelands have recently been reviewed by Jackson (1988). A list of typical birds of pine flatwoods is given in Table 10. No detailed studies exist on the birds of the old-growth southern pinelands (Jackson 1988). Two extinct species, the passenger pigeon (*Ectopistes migratorius*) and the Carolina parakeet (*Conuropsis carolinesis*), were associated with old-growth pinelands, perhaps more so in winter. The ivory-billed woodpecker (*Campephilus principalis*), considered extinct in North America by most authorities, also used old-growth pinelands as a feeding area. Therefore community structure of the avifauna of pine flatwoods has been altered since the beginning of the 20th century.

Repenning and Labisky (1985) reported 24 breeding species of birds in greater than 50-year-old longleaf pine forests of the Apalachicola National Forest, Florida. Breeding density was estimated to be 288 birds/km^2 and four species were most abundant: Bachman's sparrow (48 birds/km^2), brown-headed nuthatch (45

TABLE 8 Characteristic (X), Keystone (K), and Endemic (E) Invertebrates of Southeastern Pinelands

Species	Pine Flatwoods	Subtropical Pinelands	LLP/TO Sandhills	Sand Pine Scrub	Scrubby Flatwoods
Walking stick (*Anisomorpha buprestoides*)	X	X			
Tortoise beetle (*Hemisphaerota cyanea*)	X				
Chigger mite (*Trombicula* spp.)	X	X	X	X	X
Centipede (*Neolithobius xenopus*)	X			X	
Florida atala (*Eumaeus atala florida*)		X			
Florida leafwing (*Anaea floridalis*)		X			
Bartram's hairstreak (*Strymonacis bartrami*)		X			
Big Pine Key conehead (*Belocephalus micanopy*)		X			
Keys short-winged conehead (*B. sleighti*)		X			
Scarab beetle (*Ataenius superficialis*)		XE			
Tree snail (*Liguus* spp.)		XE			
Rosemary wolf spider (*Lycosa ericeticola*)			XE		
Wolf spider (*L. ammophila*)			X		
Scarab beetle (*Ataenius sciurus*)			X		
Lake Placid funnel wolf spider (*Sosippus placidus*)			X	X	
McCrone's burrowing wolf spider (*Geolycosa xera*)			XE	XE	
Grandaddy longlegs (*Leiobunum aurugineum*)			X		
Southern harvester ant (*Pogonomyrmex badius*)			X	X	X
Centipede (*Scolopendra viridis*)			X		
Millipede (*Abacion lactarium*)			X	X	
Red widow spider (*Latrodectus bishopi*)				XE	
Florida sand cockroach (*Arenivaga floridensis*)				XE	
Jumping spider (*Phidippus xerus*)				XE	
Rosemary bird grasshopper (*Schistocerca ceratiola*)				XE	
Grasshopper (*Melanoplus forcipatus*)			XE	XE	
Flea (*Polygenis floridanus*)			XE	XE	

Source. Adapted from Franz (1982), Peck and Howden (1985), Corey (1988), Corey and Taylor (1988), Degrup (1989), Lazell (1989), Corey and Stout (1990 and unpublished data).

TABLE 9 Characteristic (X), Keystone (K), and Endemic (E) Amphibians and Reptiles of Southeastern Pinelands

Species	Pine Flatwoods	Subtropical Pinelands	LLP/TO Sandhills	Sand Pine Scrub	Scrubby Flatwoods
Eastern diamondback rattlesnake (*Crotalus adamanteus*)	X	X	X	X	X
Black racer (*Coluber constrictor*)	X	X	X	X	X
Ground skink (*Scincella lateralis*)	X	X	X	X	
Eastern box turtle (*Terrapene carolina*)	X	X			
Chorus frog (*Pseudacris* spp.)	X	X			
Cricket frog (*Acris* spp.)	X				
Pine woods tree frog (*Hyla femoralis*)	X		X		
Narrow-mouthed toad (*Gastrophryne carolinensis*)	X		X		
Oak toad (*Bufo quercicus*)	X	X	X		
Flatwoods salamander (*Ambystoma cingulatum*)	X				
Miami black-headed snake (*Tantilla oolitica*)		XE			
Pigmy rattlesnake (*Sistrurus miliarius*)		X			
Eastern indigo snake (*Drymarchon corais*)	X	X	X		
Southeastern five-lined skink (*Eumeces inexpectatus*)		X	X	X	
Green anole (*Anolis carolinensis*)	X	X		X	
Southern chorus frog (*Pseudacris nigrita*)		X			
Spadefoot toad (*Scaphiopus holbrooki*)			X	X	
Gopher frog (*Rana areolata*)			X	X	X
Gopher tortoise (*Gopherus polyphemus*)			XK	XK	XK
Fence lizard (*Sceloporus undulatus*)			X		
Grass lizard (*Ophisaurus* spp.)			X		
Short-tailed snake (*Stilosoma extenuatum*)			X	X	
Pine snake (*Pituophis melanoleucus*)	X		X		

TABLE 9 ***(Continued)***

Species	Pine Flatwoods	Subtropical Pinelands	LLP/TO Sandhills	Sand Pine Scrub	Scrubby Flatwoods
Crown snake (*Tantilla* spp.)	X		X	X	
Sand skink (*Neoseps reynoldsi*)				XE	XE
Six-lined racerunner (*Cnemidophorus sexlineatus*)			X	X	X
Mole skink (*Eumeces egregius*)			XE	XE	XE
Hognosed snake (*Heterodon* spp.)				X	
Scrub lizard (*Sceloporus woodi*)				XE	XE
Coachwhip (*Masticophis flagellum*)			X	X	X

Source. Adapted from Carr (1940), Campbell and Christman (1982), Dodd and Charest (1988), and Dalrymple (1988).

TABLE 10 Characteristic (X), Keystone (K), and Endemic (E) Birds of Southeastern Pinelands

Species	Pine Flatwoods	Subtropical Pinelands	LLP/TO Sandhills	Sand Pine Scrub	Scrubby Flatwoods
Rufous-sided towhee (*Pipilo erythrophthalmus*)	X	X		X	X
Carolina wren (*Thryothorus ludovicianus*)	X			X	X
Common yellowthroat (*Geothlypis trichas*)	X				
Northern cardinal (*Cardinalis cardinalis*)	X		X		
Red-shouldered hawk (*Buteo lineatus*)	X	X			
Wild turkey (*Meleagris gallopavo*)	X	X			
Bobwhite (*Colinus virginianus*)	X	X	X		
Southern bald eagle (*Haliaeetus leucocephalus*)	X				
Red-cockaded woodpecker (*Picoides borealis*)	XE	XE	XE		
Red-bellied woodpecker (*Melanerpes carolinus*)	X	X	X	X	
Pine warbler (*Dendroica pinus*)	X	X	X		
Brown-headed nuthatch (*Sitta pusilla*)	X	X	X		
Bachman's sparrow (*Aimophila aestivalus*)	X		X		
Yellow-throated warbler (*Dendroica dominica*)	X				
Chuck-will's widow (*Caprimulgus carolinensis*)	X			X	X
American kestrel (*Falco sparvarius*)		X	X		
Red-tailed hawk (*Buteo jamaicensis*)	X	X			
Blue-gray gnatcatcher (*Polioptila caerulea*)			X		
Summer tanager (*Piranga rubra*)		X	X		
Red-headed woodpecker (*Melanerpes erythrocephalus*)		X	X		
Gray kingbird (*Tyrannus dominicensis*)		X			
Great-crested flycatcher (*Myiarchus crinitus*)		X	X	X	X
White-eyed vireo (*Vireo griseus*)			X	X	X
Florida scrub jay (*Aphelocoma coerulescens*)				XE	XE

Source. Adapted from Woolfenden (1969, 1970), Robertson and Kushlan (1974), Jackson (1988), and Breininger and Schmalzer (1990).

birds/km^2), and blue jay and red-cockaded woodpecker (36 birds/km^2 each). Winter bird density (321 birds/km^2) exceeded summer densities but included only 17 species. The most abundant species were pine warblers (75 birds/km^2), yellow-rumped warblers (73 birds/km^2), and eastern meadowlarks (46 birds/km^2). The number of bark (n = 6) and ground (n = 10) foraging species outnumbered the foliage gleaning (n = 4) and aerial foraging (n = 4) species during the breeding season. A similar ranking of foraging guilds was noted in the winter; however, no aerial foragers were present.

Summer resident bird populations were studied in wet flatwoods dominated by slash pine in southeast Georgia (Johnson and Landers 1982). In naturally regenerated stands 21–28 years old, 12–14 species were encountered on transects. Stands burned 2 years prior to the study yielded 217 birds/km^2, while those burned 3-5 years earlier supported 333 birds/km^2. Eighteen species were observed of which the most abundant were eastern wood pewee, brown-headed nuthatch, and pine warbler.

Analysis of avian guilds in south Florida slash pine flatwoods indicated the bird community was dominated by insectivores in the winter and by granivores in the summer (Hirth and Marion 1979). There were relatively few omnivorous or carnivorous species observed in this habitat type. Great horned owls were generally common in open pine flatwoods. Emlen (1978) presented evidence and a hypothesis to explain his observation that the density of winter migrants in pine flatwoods declined distally from the Coastal Plain toward south Florida.

The red-cockaded woodpecker was formerly distributed throughout the old-growth southern pine forests, including pine flatwoods (Jackson 1988). This species is unusual among cavity-nesting birds in that it only excavates cavities in large (old) living longleaf and slash pines. Loss of old-growth pinelands throughout the former range of the red-cockaded woodpecker has resulted in its listing as an endangered species by the U.S. Department of Interior. Details concerning the evolution, ecology, behavior, and management of the species were summarized in Thompson (1971) and Wood (1983). Jackson et al. (1985) presented a cogent argument for a greater emphasis on the use of favorable fire regimes to manage designated wilderness areas to ensure the survival of existing colonies of red-cockaded woodpeckers.

Typical mammals of pine flatwoods are listed in Table 11. No species of mammals were limited in their distribution to pine flatwoods as a habitat type; most taxa would be classified as habitat generalists. The larger the body size, the greater the number of habitats likely to be used in the course of the life cycle.

Bison (*Bison bison bison*) were historically associated with pine savannas of the southeastern Coastal Plain. Their extirpation in the region was probably completed by the early 19th century (Ehrhart 1979). The major remaining herbivores were the white-tailed deer and cotton rat. Export of hides of white-tailed deer in the period 1513–1822 suggested large numbers of individuals were present (Wing 1965); the species remains common to abundant throughout the Coastal Plain. Cotton rats were numerically dominant among the rodents of pine flatwoods studied by Layne (1974a and references therein) and Stout (1979). Sherman's fox squirrel reached its greatest abundance in regularly burned pine savannas (Moore 1957, Weigl et al. 1989). Weigl et al. (1989) have pointed out these squirrels require old-growth stands of longleaf and slash pine for survival.

Large mammalian predators were lost from the community structure of pine flatwoods as European settlers dispersed through the Coastal Plain. Panther and gray and red wolves (*Canis lupus* and *C. rufus*) were quickly extirpated or limited to the most remote areas.

TABLE 11 Characteristic (X), Keystone (K), and Endemic (E) Mammals of Southeastern Pinelands

Species	Pine Flatwoods	Subtropical Pinelands	LLP/TO Sandhills	Sand Pine Scrub	Scrubby Flatwoods
Raccoon (*Procyon lotor*)	X	X	X		
Opossum (*Didelphis virginiana*)	X	X	X		
Cottontail rabbit (*Sylvilagus floridanus*)	X	X		X	
Cotton rat (*Sigmodon hispidus*)	X	X	X		
Gray fox (*Urocyon cinereoargenteus*)	X	X	X		
Bobcat (*Felis rufus*)	X	X	X	X	X
Armadillo (*Dasypus novemcinctus*)	X				
White-tailed deer (*Odocoileus virginianus*)	X	X	X	X	
Black bear (*Ursus americanus*)	X				
Florida panther (*Felis concolor*)		X			
Cotton mouse (*Peromyscus gossypinus*)	X	X		X	X
Short-tailed shrew (*Blarina* spp.)		X			
Florida mouse (*Podomys floridanus*)			XE	XE	XE
Old field mouse (*Peromyscus polionotus*)			X	X	X
Pocket gopher (*Geomys pinetis*)			X		
Sherman's fox squirrel (*Sciurus niger shermani*)	XE		XE		
Big Cypress fox squirrel (*S. n. avicennia*)		XE			
Spotted skunk (*Spilogale putorius*)				X	X

Source. Adapted from Layne (1974a,b) and Lazell (1989).

Bobcats have remained fairly ubiquitous in pine flatwoods as the largest functional predator. Longtailed weasels persisted but at low densities and the species (*Mustela frenata olivacea* and *M. f. peninsulae*) remain poorly studied in the region (J. Hovis, personal communication).

Omnivorous black bears in contemporary populations tend to live in dense, forested wetlands adjacent to pine flatwoods, which they enter to forage for mast of saw palmetto and oaks (Maehr and Brady 1984).

The introduced feral hog (*Sus scrofa domesticus*) has a significant impact on longleaf pine regeneration (Lipscomb 1989).

Successional Dynamics Pine flatwoods have undergone extensive manipulation and alteration, such as controlled burning, site conversion to pine plantations, and clearcut harvesting. All these perturbations change the structure and the function of pinelands and their attractiveness to wildlife. Marion and Harris (1982) discussed in some detail the implications for wildlife of increasing forest productivity in flatwoods of the southeastern Coastal Plain.

Just as fire plays an important role in shaping and maintaining this plant association, it also is a dominant factor influencing the composition and dynamics of animal communities (Bendell 1974). Burning has multiple effects on both the *structure* (e.g., species composition, biomass, foliage height diversity) and *function* (e.g., primary productivity, rates of nutrient cycling, wildlife habitat value) of this community. A number of studies have documented the effects of fire on wildlife as variable depending on the species being considered, frequency of burning, extent of coverage, and conditions under which burning occurred. A summary of the topic was presented by Wood (1981).

Buckner and Landers (1980) predicted a sequence of vegetational development following burning in upland pines of the southeastern Coastal Plain. They reported that certain frequencies of burning were important for developing suitable habitat conditions for wildlife. Recommendations included a 1–2 year burning schedule to favor bobwhites and a 3–5 year burning interval to allow development of browse and cover plants (suppressed by 1–2 year burns) of good quality forage for deer, which would allow enough accumulation of fuel to support the next prescribed burn. Additionally, the 3–5 year burning schedule seems to be quite compatible with those suggested for silvicultural purposes.

Subtropical Pine Forest The fauna of the subtropical pine forests was derived from the southeastern Coastal Plain; however, species richness is reduced relative to the other pinelands of this region. Differentiation of mainland forms along the keys archipelago has resulted in many subspecies, some of which are restricted to these pinelands. In contrast, the fauna of the rockland pinelands on the mainland has evolved without isolation from more northern forms of their respective taxa. Urban and agricultural development has resulted in significant loss and fragmentation of these habitats with the attendant reduction and isolation of the biota.

Characteristic Animals Among the invertebrates of these pinelands, those that bite or otherwise annoy people (mosquitoes, chiggers, and roaches) are best known. Comprehensive studies of invertebrate community structure and function remain to be done. Examples of invertebrates associated with subtropical pine forests are given in Table 8. Development of private land or lack of management on public lands may further endanger the future of the Florida atala, Florida leafwing, and the Big Pine Key conehead grasshopper (Franz 1982). Peck and Howden (1985) studied scavenging beetles (scarabs) in the keys. Their data indicated Big Pine Key (17.19 km^2), where extensive subtropical pinelands occur, supported 14 species of scarabs; most of the other keys where pinelands are absent harbored 1–3 species.

Characteristic species of reptiles and amphibians of the subtropical pinelands are given in Table 9. Dalrymple (1988) reported a study of the herpetofauna of the Long Pine Key region of Everglades National Park. In pinelands he observed 30 species: 7 anurans, 2 turtles, 6 lizards, and 15 snakes. Based on 2550 herp array days, 292 amphibians and reptiles were captured in the pinelands. Among the 22 species captured, 73.5% of the individuals were accounted for by the green anole (n = 136), black racer (n = 30), and southern toad (n = 24). Descriptive accounts in Lazell (1989) suggested 5 anurans, the box turtle, 2 lizards, and 5 snakes comprised the herpetofauna of slash pine flatwoods on Big Pine Key. Thus keys pinelands supported 17 fewer species than Long Pine Key. The rare Miami black-headed snake is endemic to sandy soils over oolitic limestone and may occur in pinelands or tropical hammocks (McDiarmid 1979, Lazell 1989).

The birds of the subtropical pinelands have been discussed in detail by Robertson (1955) and Robertson and Kushlan (1974) (Table 10). About 300 species of birds naturally occur in southern Florida. However, the number of land breeding birds is reduced from 40 to 20 from the northern to southern extent of subtropical pinelands. About 18 birds formerly reached the southern limit of their breeding ranges in these pinelands. Pinelands of the mainland are the primary habitat for bobwhite, eastern kingbird, eastern bluebird, pine warbler, common grackle, summer tanager, and blue jay. Of this subset, only the common grackle occurs in pinelands of the keys. The ivory-billed woodpecker and Carolina parakeet are extinct, while the American kestrel no longer breeds at Long Pine Key (W. B. Robertson, personal communication). Red-cockaded woodpeckers occur in the old-growth pinelands of the Big Cypress Preserve but have been extirpated at Long Pine Key (Patterson and Robertson 1981). Typical breeding birds in pinelands on Big Pine Key include red-bellied woodpeckers, northern cardinals, and gray kingbirds.

Both the number of species and the density of breeding birds are reduced in subtropical pinelands relative to pine flatwoods of the southeastern Gulf Coastal Plain. For example, breeding bird density at Long Pine Key was reported to be 55–56 breeding males/40 ha (1.38/ha), while 5–6 breeding males/40 ha (0.14/ha) were recorded at Big Pine Key (Robertson and Kushlan (1974). These densities contrast markedly with those reported for pine flatwoods elsewhere (2.88/ha) (Repenning and Labisky 1985).

Layne (1974b) characterized south Florida, including the subtropical pinelands, as being deficient of rodents and bats relative to the rest of Florida. In contrast, mammalian carnivores were fully represented. Among the 35 species of mammals found in the region, as many as 50 subspecies have been reported (Layne 1974b). Lazell (1989) elaborated on the role of isolation in the formation of races among mammals of the keys.

Development and human population growth have resulted in the extirpation of the red wolf and reduction in abundance and range of the black bear and Florida panther (Layne 1974b, Brady and Maehr 1985).

Selected mammals of the subtropical pinelands are listed in Table 11. Raccoons and cotton rats may be the most abundant mammals in the pinelands (Layne 1974b). Typical mammals in pinelands on Big Pine Key would include cotton rats, opossum, raccoon, and key deer. The Big Cypress fox squirrel is largely restricted to southwest Florida, where it occupies subtropical pine forest in Big Cypress National Preserve as well as other habitats in the region (Williams and Humphrey 1979).

The key deer, as a unique feature of pinelands of the lower keys, is succinctly characterized by Klimstra and Hardin (1979). This insular form of the white-tailed deer is classified as endangered by the U.S. Fish and Wildlife Service and protected in the Key Deer National Wildlife Refuge, Big Pine Key, Florida.

Successional Dynamics Alexander (1958, 1967) has documented the potential for the rapid conversion of subtropical pinelands to tropical hammock when fire is excluded as a natural feature. Alexander and Dickson (1970, 1972) studied vegetation dynamics on the Key Deer National Wildlife Refuge relative to fire and its use to improve the growing condition for browse plants. They noted a general lack of information on these pinelands and their reaction to fire.

A lack of fire on a regular basis (every 3–5 years), coupled with disturbance of the surface limestone, makes subtropical pinelands susceptible to invasion by exotic plants. Ewel et al. (1982) discussed the invasion of pinelands by *Schinus terebinthifolius*. The problem with exotic plant invasion is far more serious, however; Whiteaker and Doren (1989) listed 221 species of introduced plants that occur in the Everglades National Park, many of which may invade the pinelands.

Very little information is available on the impact of exotic plant invaders on the pinelands fauna. Mazzotti et al. (1981) trapped small mammals in stands dominated by either *Melaleuca quinquenervia* or *Casuarina equisetifolia*. Cotton mice, cotton rats, and rice rats (*Oryzomys palustris*) were found in both habitats, with more captures in *Melaleuca* than *Casuarina* stands. Further work in *Melaleuca* stands by Sowder and Woodall (1985) suggested very low numbers of cotton mice and rats were present. Unfortunately, neither of these studies cited any study of pinelands as a control for the sake of comparison. Worth (1950) reported trapping for rodents in Long Pine Key; however, no captures were made. He speculated this was because no ground cover was present (probably because of frequent fires).

Emlen (1970) studied the response of birds to controlled burning of 20-year-old slash pine on Long Pine Key. He was unable to detect any difference in composition or abundance of resident birds on adjacent burned and unburned plots.

Longleaf Pine–Turkey Oak Sandhills Animals of this community are typically adapted to extremely harsh microhabitat conditions, such as high temperatures and drought. To avoid these extremes and to prevent some water loss, many of the animals are burrowers.

Characteristic Animals Invertebrates of longleaf pine–turkey oak sandhills have generally been characterized in recent years (Table 8). Reiskind (1987) reported on the local distribution of the rosemary wolf spider, a taxon known only from sandhills with an understory of rosemary (*Ceratiola ericoides*) in Putnam County, Florida. Arachnids of sandhills in north and central Florida were documented by Corey and Stout (1990). The most common ground surface spider was *Lycosa ammophila* (Corey et al. in preparation). Southern harvester ants are conspicuous in sandhills (McCoy and Kaiser 1990). Kalisz and Stone (1984b) showed that from 3990–9670 kg/ha/yr of soil was brought to the surface by the combined action of the scarab beetle (*Peltotrupes youngi*) and pocket gophers. A recent compilation of invertebrates considered to be burrow commensals with the gopher tortoise listed 302 species [e.g., the gopher tortoise tick (*Amblyomma tuberculatum*), cave crickets (*Ceuthophilus latibuli* and *C. walkeri*), dung beetles (*Onthophagus* spp.), and scat flies (*Eutrichota gopheri*)] (Jackson and Milstrey 1989).

The herpetofauna of sandhills has been described in Carr (1940), Campbell and Christman (1982), Dodd and Charest (1988), and Stout et al. (1988). Typical taxa are listed in Table 9. In excess of 60 species of reptiles and amphibians may be associated with the sandhill biotope. Those especially adapted to the xeric conditions of the habitat include the mole skink, sand skink, eastern coachwhip, short-tailed snake, southeastern crowned snake, and six-lined racerunner (Campbell and Christman 1982).

The gopher tortoise and its burrow are widely recognized as keystone features of the sandhill community (Stout 1981, Eisenberg 1983, Kaczor and Hartnett 1990). Active and abandoned tortoise burrows shelter a commensal fauna of 60 vertebrates (e.g., pine snake, eastern indigo snake, gopher frog, and Florida mouse) and 302 invertebrates (Jackson and Milstrey 1989). Pocket gopher (*Geomys*) mounds and, to a lesser extent, their burrows represent an additional key microhabitat for burrowing species of amphibians and reptiles (Funderburg and Lee 1968).

Three fossorial, insectivorous reptiles, namely, the southeastern crowned snake (*Tantilla relicta*), the mole skink (*Eumeces egregius*) and the sand skink (*Neoseps reynoldsi*), comprise a unique "sand swimming" guild (Smith 1982). Differences in activity with respect to soil depth among the species and corresponding differences in prey item selection appear to explain local coexistence.

Temporary ponds within the longleaf pine–turkey oak sandhill community represent an ephemeral but critical habitat for many elements of the sandhill fauna. Moler and Franz (1988) reported 16 anuran species breeding in these wetlands; success of breeding efforts was greatest in small ponds that lacked populations of predatory fish and certain predatory insects. During 27 months of study, Dodd and Charest (1988) captured 39 species (7161 individuals) of reptiles and amphibians from a single 0.16-ha pond adjacent to sandhills in north Florida. Striped newts (*Notophthalmus perstriatus*) and eastern narrow-mouthed toads (*Gastrophryne carolinensis*) were the most commonly captured amphibians. Bailey (1990) reported a study of the gopher frog at a breeding pond in south-central Alabama.

Jackson (1988) has cautioned that no data exist on the composition and abundance of the bird populations associated with the old-growth pinelands of the southeast. Certainly this is true with respect to the longleaf pine–turkey oak sandhills. Characteristic birds are listed in Table 10. Comparative lists of breeding birds reported by various authors are summarized in Table 12. The number of

TABLE 12 Breeding Birds (X) Recorded from Representative Study Sites Within the Sandhills of Florida and Georgia

Species	Slash Pine–Turkey Oak[a]	Longleaf Pine–Turkey Oak 1960[b]	Longleaf Pine–Turkey Oak 1988[c]	Longleaf Pine–Turkey Oak 1981[d]
Rufous-sided towhee	X(A)			X(A)
Blue jay	X(A)			X
Mourning dove	X		X	X
Chuck-will's-widow	X			
Red-bellied woodpecker	X(C)	X	X	X
Great-crested flycatcher	X(C)	X	X	X
Florida scrub jay	X			
Yellow-shafted flicker	X(C)			X
American kestrel	X(C)			
Great horned owl	X			
Fish crow	X			
Blue-gray gnatcatcher		X(A)	X	
Summer tanager		X(A)	X	X
Tufted titmouse		X	X	X
Yellow-throated vireo		X(C)		X
Bobwhite		X		X
Downy woodpecker	X(C)	X(C)	X(C)	X(C)
Yellow-billed cuckoo		X	X	
Pileated woodpecker			X(C)	X(C)
Carolina chickadee			X(C)	
Carolina wren	X(C)		X(C)	X(C)
Northern parula		X	X	
Pine warbler			X	X(A)
Northern cardinal	X	X	X	
Red-headed woodpecker		X(C)		X
Yellow-throated warbler		X		
Common nighthawk		X		
Bachman's sparrow				X(A)
Indigo bunting				X
Wood pewee				X
Brown-headed nuthatch				X(C)
Common yellowthroat				X
Brown-headed cowbird				X
Blue grosbeak				X
Eastern meadowlark				X
White-breasted nuthatch				X(C)
Yellow-breasted chat				X
Wood duck				X
Eastern bluebird				X(C)
Red-cockaded woodpecker				X(C)
Hairy woodpecker				X(C)
Brown thrasher				X
Orchard oriole				X
Eastern kingbird				X
Loggerhead shrike				X
Number of species	14	14	14	33

Note. (A), most abundant species; (C), cavity-nesting species.

[a] Adapted from Woolfenden (1969).

[b] Adapted from Allen et al. (1960).

[c] adapted from Stout and Corey (1990).

[d] Adapted from Engstrom (1981).

breeding bird species slightly more than doubled (33) in Thomas County, Georgia, relative to Alachua County (14) and Highlands County (14), Florida. Classic old-growth pineland species such as red-cockaded woodpeckers and brown-headed and white-breasted nuthatches were missing from the sites in Florida where they are now extirpated or vastly reduced in abundance. Sixteen of the 44 species (36.3%) were cavity nesters (Table 12).

Mammals of sandhills are generally shared with other habitats in typical landscape settings (Table 11). Notable exceptions include the pocket gopher and fox squirrel. Pocket gophers are generally limited to the sandhill biotope. Their burrow system supports an assemblage of commensal species, most of whom are not shared with the burrow system of gopher tortoises (Young and Goff 1939). Pine snakes may be the major predator on pocket gophers. Long-tailed weasels have also been observed leaving pocket gopher burrows (Moore 1945).

A classic natural history study of the Sherman's fox squirrel was done by Moore in sandhill habitat at Welaka Reserve, Putnam County, Florida (Moore 1957). Recent work using radiotelemetry yielded minimum convex polygon estimates of home ranges as 40.0 ha for males and 20.6 ha for females in sandhills of the Ordway Preserve, Putnam County, Florida (Kantola 1986). Using similar methods, Weigl et al. (1989) reported 26.6 ha for males and 17.2 ha for females in North Carolina. These studies underscore the large expanses of habitat needed to support viable populations.

Typical small mammals reported from live-trapping studies in sandhills include old field mice, cotton rats, Florida mice, and cotton mice (Moore 1946, Barrington 1949, Pournelle 1950, Arata 1959, Stout and Corey 1990). A paucity of captures was typical; for example, Pournelle caught two cotton mice out of 850 trap nights. Stout and Corey (1990) used drift fences and pitfall traps to reveal short-tailed shrews (*Blarina carolinensis*) on 6 of 12 sandhill study sites.

Moore (1949) reported a gray fox den constructed from a gopher tortoise burrow. Landers and Speake (1980) reported an extensive list of medium and small mammals found in tortoise burrows in Georgia.

Successional Dynamics Plant biomass accumulation was rapid enough in most sandhill habitats to require prescribed burns every 2–4 years (Landers and Speake 1980). In Georgia, gopher tortoise abundance (15.8/ha) was greater in a longleaf pine–turkey oak stand burned at those intervals than in an otherwise comparable site (3.3/ha) that had been fire-free for 8 years. Slash pine plantations subjected to frequent burns yielded twice as much herbaceous biomass, triple the number of tortoises, and nearly triple the number of observations of eastern indigo snakes as an adjacent longleaf pine stand that was rarely burned (Landers and Speake 1980). In Florida sandhills, 1-ha plots burned at 1 and 7 year intervals supported a more diverse herptofauna than did plots burned biannually or not burned (Mushinsky 1985). Campbell and Christman (1982) observed that herpetofaunal diversity and abundance decreased as pines mature and/or as ground cover increased.

McCoy (1987) found no direct effect of fire on ground beetles in Florida sandhills. However, fire did influence vegetative structure and the vulnerability of beetles to predation. The southern harvester ant responded to fire by increasing the number of individuals emerging from colony entrances and by foraging over larger areas (McCoy and Kaiser 1990).

Intensive forestry in sandhill habitats involves clearcutting, site preparation, and planting. Umber and Harris (1974) reported on the effects of clearcutting 50, 75, and 100% of nine 259-ha plots relative to three 259-ha control plots. Site preparation increased ground cover of grass and forbs relative to the controls and gopher tortoises and ground-level arthropods were more abundant ($p < 0.05$) in the plantations than in the controls. Fox squirrels and nongame birds were more abundant in the control plots than in the plantation plots. Conversion of longleaf pine stands to slash pine plantations was judged to be undesirable (Umber and Harris 1974). Site preparation such as double chopping eliminated oak reproduction and wiregrass (Hebb 1971). Diemer and Moler (1982) demonstrated that gopher tortoises may survive chopper-type forest site preparation. Pine plantations tended to be younger than native forests and averaged 25% as many den trees as naturally regenerated stands (McComb et al. 1986).

Arata (1959) reported on the response of small mammals to a midwinter burn in a longleaf pine–turkey oak stand. Old field mice and Florida mice continued to occupy the burned area without a change in abundance. In contrast, cotton rats appeared to shift to adjacent, unburned habitat. Gates and Tanner (1988) examined the effects of prescribed burning on pocket gophers and their food plants. Mounding activity of the gophers was not affected by the fires. Carbohydrate and nitrogen levels of the roots of selected plants were not clearly influenced by the burns.

Restoration of sandhill communities was discussed by Humphrey et al. (1985). Diemer (1986) described restocking tortoises on sites where local populations had been extirpated. Experiments with eastern indigo snakes have proved that locally extirpated species may be successfully reintroduced in suitable sandhill habitat (Speake et al. 1987).

Sand Pine Scrub Sand pine scrub is perhaps the most ancient terrestrial plant community in the southeastern United States. Its antiquity, coupled with its spatial distribution as an archipelago of relatively discrete habitat islands, suggests *a priori* a fauna characterized by specialization and endemism.

Characteristic Animals The invertebrates or arthropods of sand pine scrub have not been analyzed as to species composition and ecological relationships. Selected species reported from sand pine scrubs are listed in Table 8. Deyrup (1989) reported on the arthropods endemic to Florida scrub with emphasis on the central ridges, especially the Lake Wales Ridge. He reported 46 species and noted the proportion of endemics was not necessarily unusual. For example, of 59 species of ants found in the scrub, only 3 were considered scrub endemics. Species composition and relative abundance of ground surface spiders (Corey and Taylor 1988), foliage-dwelling spiders (Corey and Taylor 1989), and centipedes and millipedes (Corey 1988) of central Florida scrub have been documented. Kalisz and Stone (1984b) studied soil mixing by the scarab beetle (*Peltotrupes youngi*) in sand pine scrubs of the Ocala National Forest. Tenebrionidae larvae were the principal prey of *Tantilla relicta* (Smith 1982).

A rich diversity of amphibians and reptiles is associated with sand pine scrub. Selected species are listed in Table 9. Results of trapping in a variety of xeric and mesic habitat types revealed more species of amphibians and reptiles in scrub (21) than in hydric hammock (17), which was the next richest habitat (Campbell and Christman 1982). Nonetheless, all the species (24) listed from scrubs by Christman et al. (1979) were also known to occur in longleaf pine–turkey oak sandhill sites. The gopher tortoise acts as a keystone species with regard to the burrow commensals (see section on fauna of sandhills). Herpetofaunal elements most closely associated with scrub of the central ridge of Florida include the scrub lizard, blue-tailed mole skink (*E. e. lividus*), sand skink, peninsula crowned snake (*T. r. relicta*), and short-tailed snake (Layne 1990). Disjunct scrubs of the Atlantic Coast contain scrub lizards and the coastal dunes crowned snake (*T. r. pamlica*). None of the herpetofaunal endemics is found in the disjunct scrubs along the northern Gulf coast (Layne 1990). Enge et al. (1986) reported on the local distribution and population status of the scrub lizard within its known geographic range.

Species composition of breeding and wintering birds of sand pine scrub is influenced by the areal extent of the habitat islands and the time elapsed since the last fire. Recovery of the sand pine canopy and the evergreen shrub layer depends on the conditions that prevailed during the most recent fire and in the subsequent two to three growing seasons. Characteristic birds of sand pine scrub are listed in Table 10. Woolfenden (1969) studied an 8.09-ha example of sand pine scrub, two-thirds of which was supporting sand pine 12–15 m in height. The species of breeding birds included rufous-sided towhee, blue jay, chuck-will's-widow, Carolina wren, great-crested flycatcher, white-eyed vireo, red-bellied woodpecker, hairy woodpecker, and northern cardinal. The number of breeding males was estimated to be 80/40 ha. Wintering birds on the same study site included 25 species with an estimated density of 390/40 ha. Among the wintering birds, rufous-sided towhees, ruby-crowned kinglets, and blue-grey gnatcatchers were most commonly observed (Woolfenden 1970). Florida scrub jays do not typically occupy sand pine scrub after the regrowth of the vegetation may be described as tall and dense (Woolfenden and Fitzpatrick 1984, p. 40). (See the section on scrubby flatwoods for more details on the scrub jay.)

The Florida mouse is the only mammal that might be claimed to be largely restricted to sand pine scrub where it is a facultative commensal with the gopher tortoise (Layne 1990). Other mammals utilize scrub and adjacent xeric communities and must be considered as habitat generalists (Table 11). Typical small mammals in scrub included Florida mice, cotton mice, golden mice (not south of Lake Okeechobee), flying squirrels, and gray squirrels (Stout 1982, Layne 1990). The old field mouse occurs in scrubs of the northern Gulf coast, north-central, and central ridge of Florida. The Florida mouse occurs as a disjunct population in Franklin County but does not occupy scrubs farther west along the Florida or Alabama Gulf coast (Layne 1979). The spotted skunk inhabits scrubs of the central ridge and of the Atlantic coast. Bobcat and gray fox frequent scrub, but their individual home ranges encompass considerable habitat variation (Wassmer et al. 1988).

Successional Dynamics Faunal response to periodic timber harvest of sand pine scrub, as is practiced in the Ocala National Forest, is poorly understood (Stout et al. 1988). Christman et al. (1979) studied the response of the herpetofauna to clearcutting and replanting on the Ocala National Forest. Their chronosequence included sites replanted 1, 3, 5, 7, 16, and 33 years prior to study. Total herpetofaunal abundance decreased as stands aged. Shifts in the numerically dominant taxa were associated with open and closed canopy conditions. Scrub jays abandoned territories as regrowth and canopy formation occurred in scrubs of the central ridge (Woolfenden and Fitzpatrick 1984). The response of the avifauna in general to structural changes in sand pine scrub has not been documented. The Florida mouse continued to occur in sand pine scrubs that had been free of disturbance for more than 60 years (J. N. Layne, personal communication); however, early stages of recovery appeared to support greater densities of the species (Stout et al. 1988).

Scrubby Flatwoods The fauna of scrubby flatwoods is generally poorly studied; however, certain species (e.g., the Florida scrub jay) have been studied intensely in this habitat (Woolfenden and Fitzpatrick 1984). Many, if not most, animals indigenous to scrubby flatwoods also inhabit sand pine scrub and drier phases of pine flatwoods. The well-drained soils support a sparse assemblage of grasses and herbs not found in sand pine scrub. This subtle difference in the two habitats favors herbivores such as gopher tortoises and cotton rats.

Characteristic Animals Invertebrates associated with examples of scrubby flatwoods are poorly known (Table 8). Deyrup (1989) has discussed arthropods endemic to Florida scrub. His ongoing research will ultimately reveal the similarities and differences among the various scrub biotopes, to include scrubby flatwoods.

Amphibians and reptiles that may be expected in scrubby flatwoods are indicated in Table 9. This list is conservative and unpublished work by James N. Layne, among others, will clarify the similarity of the herpetofauna of scrubby flatwoods and sand pine scrub. The relative treeless nature of many scrubby flatwood stands suggests surface temperature extremes during the summer months may favor fossorial forms (e.g., sand skinks) over surface active forms such as the six-lined racerunner.

Few data are known to exist on the bird species composition of scrubby flatwoods (Table 10). Woolfenden (1969) reported 13 species as breeding in an 8-ha study area on the Archbold Biological Station, Highlands County, Florida. The four most abundant species were the rufous-sided towhee, Florida scrub jay, great-crested flycatcher, and blue jay. Territorial males were estimated to number 125/40 ha. A nearby recently burned (3 years postburn) scrubby flatwoods supported 12 species of breeding birds (Woolfenden 1969). Species composition was altered relative to the unburned site and the five most abundant birds were rufous-sided towhee, ground dove, bobwhite, Florida scrub jay, and eastern meadowlark. The number of breeding males was estimated as 50/40 ha. Wintering birds were reported to differ slightly in species composition in unburned scrubby flatwoods relative to the breeding birds. Among the most abundant species were rufous-sided towhee, Florida scrub jay, common yellowthroat, and northern mockingbird (Woolfenden 1970); however, total numbers of wintering birds were similar to total numbers of breeding birds. The recently burned scrubby flatwoods supported more wintering birds than did the unburned site.

Breininger and Schmalzer (1990) reported on the composition and abundance of breeding and wintering birds of a scrub type (similar to scrubby flatwoods) from Brevard County, Florida. The most common breeding birds included rufous-sided towhee, Carolina wren, white-eyed vireo, and Florida scrub jay. Based on birds/ha, the four most common species in winter were yellow-throated warbler, rufous-sided towhee, Carolina wren, and white-eyed vireo.

The Florida scrub jay may be the animal most symbolic of scrubby flatwoods. It is arguably most abundant in the low (0.5–1.5 m height), open oak scrub that characterizes this vegetation type. Early recovery stages of sand pine scrub may be used by breeding pairs, but use declines as shrub height increases (Woolfenden and Fitzpatrick 1984, p. 42). Florida scrub jay density varied from 3.59 to 4.04 pairs/40 ha over a 9-year period in prime scrubby flatwoods habitat (Woolfenden and Fitzpatrick 1984). Florida scrub jays may be more dense in the oak scrub on Merritt Island than has been reported elsewhere in their range (Breininger and Schmalzer 1990).

Few data are available on the species composition or relative abundance of mammals found in the scrubby flatwoods (Table 10). Pearson (1954) reported 14 captures of cotton rats based on 209 trap nights in the vicinity of Gulf Hammock. Seasonal trapping (summer 1972 to winter 1975) of the biotope on Merritt Island, Florida, yielded captures of cotton rats, cotton mice, golden mice (*Ochrotomys nuttalli*), Florida mice, and rice rats (*Oryzomys palustris*) (Ehrhart 1976). The rice rats were taken in a wet depression (swale) included within the study area. Based on relative abundance, the rank-order of the small mammals was cotton rat, cotton mouse, Florida mouse, and golden mouse. Layne (1990) showed that Florida mice were more abundant (numbers/100 trap nights) in scrubby flatwoods than in sandhill or sand pine scrub in three (winter, summer, and fall) of four seasons.

The medium- and large-sized mammals of other pineland types (e.g., pine flatwood, scrub, and sandhill) may be encountered in scrubby flatwoods.

Successional Dynamics Few studies have reported on the disturbance of scrubby flatwoods with fire (Woolfenden 1970, Abrahamson 1984a) or mechanical clearing (Breininger and Schmalzer 1990). Recovery of canopy coverage to preburn conditions may occur within 1 year on the southern Lake Wales Ridge (Abrahamson 1984a). Woolfenden (1969) found 12 species of breeding birds on a burned (3 years postburn) scrubby flatwoods and 13 species on a nearby unburned site. However, fewer breeding males were present on the burned (50/40 ha) as opposed to the unburned (125/40 ha) study plots. Layne (1990) stated Florida mice persisted in low numbers in scrubby flatwoods last burned in 1927.

Mechanical disturbance of oak–palmetto scrub (a coastal variant of scrubby flatwoods) delayed recovery and after 20 years ground cover and openings in the shrub layer distinguished it from adjacent undisturbed and burned stands (Breininger and Schmalzer 1990). Nonetheless, the estimated number of birds/ha was greater in the disturbed habitat than in the undisturbed habitat in summer, autumn, and spring, with densities strongly reversed in winter (14.9 versus 21.8).

Scrubby flatwoods is a major habitat of the Florida scrub jay (Woolfenden and Fitzpatrick 1984). Lands designated to maintain populations of this federally threatened species must be managed to avoid habitat changes inimical to the species. The meager data now available on disturbance and recovery time of the community does not encourage the detailing of management practices beyond these general rules: (1) maintain the scrub oaks vital for the production of acorns, (2) ensure that average shrub height does not exceed 2 m, and (3) maintain shrub cover in a discontinuous pattern with sparsely vegetated openings available throughout.

RESOURCE USE AND MANAGEMENT EFFECTS

This section considers the use, development, and management of pine forests of the southeastern Coastal Plain in Florida. Chapter 10 in this volume addresses these issues for the longleaf pine forests of the entire Coastal Plain.

The history of use of natural resources associated with pine forests of the southeastern Coastal Plain began with the arrival of European immigrants. In contrast, the Florida peninsula, especially southern Florida, was one of America's last frontiers. Conflicts with Native Americans, presence of seemingly impenetrable swamps and marshes, alligators, mosquitoes, and their associated diseases, all delayed the early use and development of Florida's pine resources. Only in the past 100 years have transportation networks penetrated into subtropical regions of Florida. Growth and development in Florida in the last several decades have more than compensated for any slow beginnings.

Use and Development of Florida Pine Forests

Pinelands of the southeastern Coastal Plain have had four major uses in recent history: (1) production of timber and pulpwood, (2) naval stores, (3) cattle grazing, and (4) recreation. In 1900, cattle grazing was easily the most important use of these lands, followed in importance by naval stores, timber, pulpwood, and recreation (Florida Department of Agriculture 1906, Brown 1909). Much of the forest was pristine because poor road systems did not allow access into interior forests. Also, in the early 1900s, the extensive use of wood in phosphate mining operations (Fig. 10) was thought to be locally important in central and northern Florida. More recently, the mining of phosphate underneath pine forests has had negative impacts on the forest resources because former forests were converted to pasture. Additionally, conversion of pinelands to urbanized areas, much of it unplanned from a resource management perspective, has taken a major toll in recent years. For example, while there are still large pineland areas remaining, certain unique areas have been destroyed, such as slash pine forests of the Miami rock ridge. This once forested region has now been converted into the highly urbanized cities of Miami, Fort Lauderdale, and West Palm Beach.

FIGURE 10. Phosphate mining in pine flatwoods near Bartow, Florida circa 1900. (Courtesy of Florida Institute of Phosphate Research.)

The Role of Transportation in Early Development

Development and use of natural resources found in Coastal Plain pine forests depended on good transportation networks. The most important systems for delivering products from these forests were steamships and railroads (Stockbridge and Perry 1926, Fernald 1981, Cresap 1982). Navigable streams, rivers, and lakes were starting points for resource development, especially those linked with coastal ports. Tampa, Punta Gorda, and Punta Rassa-Fort Myers linked south Florida with Cuban and South American markets, particularly for beef sales (Akerman 1976). The east coast was served by the ports of Jacksonville (St. Johns River complex) and the Indian River, with access to northern U.S. markets. Lumber and cattle industries were dependent on shipping routes prior to the 1880s. Timber companies concentrated their efforts on forests most easily accessed by waterways (Brown 1909, Schultz 1983). Naval stores industries followed the same pattern but kept advancing ahead of cutting operations. South Florida cattlemen were heavy users of southern ports but were not obligated to locate near watercourses. Cattle drives were used to bring livestock to shipping points on waterways (Akerman 1976).

By 1900, railroads were starting to open new portions of the Florida frontier. In 1887, links between Punta Gorda and Tampa to railroads of northern Florida had been established (Fernald 1981); this connection allowed timber and naval stores industries to penetrate the interior of native pine forests. The cattle industry profited by a market expansion to the northern United States and by supplying beef to timber workers. Railroads also stimulated increases in phosphate exploration and production (Blakey 1973).

The Florida East Coast Railway, completed to Miami in 1896, opened the way for a new use of these forested regions—urbanization. For the first time, northerners had a convenient and safe way of reaching the tropical Florida environment. Besides luring tourists and settlers to this region, the railroad also sparked creation of agriculture, particularly winter vegetables and tropical fruit along the east coast.

There were no paved highways in south Florida at the turn of the century. Roads, many of them covered only with pine straw, served as an alternate means of travel (Sellards and Cox 1911). In 1921, there were 2116 miles (3404 km) of public roads in the entire 12-county region (old geographic county designation). One-lane brick roads were present in north Florida circa 1920 (Sam Hopkins, personal communication). Of the "improved" roads, none were paved, but a majority were covered with marl and crushed stone or shell. Roads are indicative of the spreading web of urbanization.

Cattle Industry in South Florida

The oldest use of pinelands in Florida was for grazing cattle. Scrub cattle were developed from cattle introduced by Spanish explorers in the 1500s. Before the advent of modern veterinary practices, these cattle were the only breeds that could endure the climate and environment of Florida.

The most productive rangeland with respect to cattle lies almost entirely within the range of south Florida slash pine (Fernald 1981). These forests north of the Miami ridge supported a well-developed ground cover of herbaceous vegetation. Fires promoted the growth of grasses and other forage plants, particularly prior to the summer rainy season.

Cattle ranching did not become a large-scale operation until the 1800s. As mentioned before, better transportation was an impetus for expanding the beef industry in Florida. Cuban markets were most lucrative prior to the Civil War. During the war, both armies proved to be heavy users of beef. In the period between the war and 1900, Cuba's beef market began to be slowly reestablished; this in turn allowed for expansion of the cattle industry. In 1900, transportation networks, primarily the railroad, opened up interior pineland forests for the timber and naval stores industry, whose workers also supplied a valuable market for beef. In 1905, there were an estimated 678,669 head of native scrub cattle worth about $4.11 million in the then 12-county south Florida slash pine region.

The Timber Industry

Pine forests of the southeastern Coastal Plain have long been viewed as the most important natural resources of the region (Anonymous 1868, Brown 1909, Stockbridge and Perry 1926). However, these descriptions usually referred to northern and central highland forests composed of large, virgin longleaf pines. South Florida slash pines were considered to be third rate pinelands because of their occurrence on low flatwoods sites (Anonymous 1868). Low density of trees, reduced height, scrubby form, and high water table did not create the appearance of a valuable timber resource (Brown 1909). However, at the turn of the century, longleaf pine forests of the more northern pine belt had been ravaged, which focused attention on south Florida slash pine forests (Brown 1909). By 1905, production values for timber and naval stores were $4.8 million in the 12 Florida counties containing south Florida slash pines (Census of Agriculture 1905). Although longleaf and sand pine may have occurred in this region, most of the timber was assumed to be south Florida slash pine. The contributions of cypress and hardwoods to this total were unknown.

In a report compiled for the U.S. Forest Service, Brown (1909) predicted the demise of the timber industry in Florida. No regeneration methods were being practiced to reestablish forests. Based on the 1908 rate of cutting, he predicted that the south Florida slash pine forest would last only 25 more years. However, with development of federal and state forest services, the timber resource was better managed.

Today, there are 419,838 ha of south Florida slash pine (Bechtold and Sheffield 1981). Very little of this forested area is owned or controlled by the forest industry. In Florida, 99% of the commercial holdings are in the northern counties (Bechtold and Knight 1982). Slash pine forests in south Florida cannot match the growth, quality, and quantity of more northern slash pine forests. Because of current forestry practices, including fire control and planned regeneration, northern Florida and southern Georgia are the focal points of industrial forestry in the southeast. Current forest management practices on public and private land vitiate maintenance of biodiversity due to alteration of fire regimes, habitat fragmentation, and ground cover modifications (Jackson et al. 1986).

Naval Stores Industry in the Southeastern Coastal Plain

The naval stores industry was the oldest user of southeastern pine forests (Schultz 1983). The pitch and tar produced were needed to make ships watertight and to preserve rope. Later, chemical industries needed turpentine and resins for paint products, varnishes, hand soaps, and paper (Stockbridge and Perry 1926).

Historically, the naval stores industry demonstrated a southward migration, advancing just ahead of loggers. North Carolina, South Carolina, Georgia, and finally Florida were each leading producers of naval stores into the 20th century (Fig. 11). It was not until the southern peninsula of Florida was opened by railroads that naval stores industries became important there. South Florida slash pine was recognized as an excellent naval stores producer (Brown 1909). In fact, these forests were more valued for their gum capacities than for their timber. In the south Florida region, 1905 census data indicated that $2.2 million worth of naval stores were produced. Today, production of naval stores has become unimportant as this industry has been reduced to a "small specialty industry in the U.S." (McReynolds 1983). A discussion of the history of this industry and its impact on the southeastern pine forests is also provided in Chapter 10 of this volume.

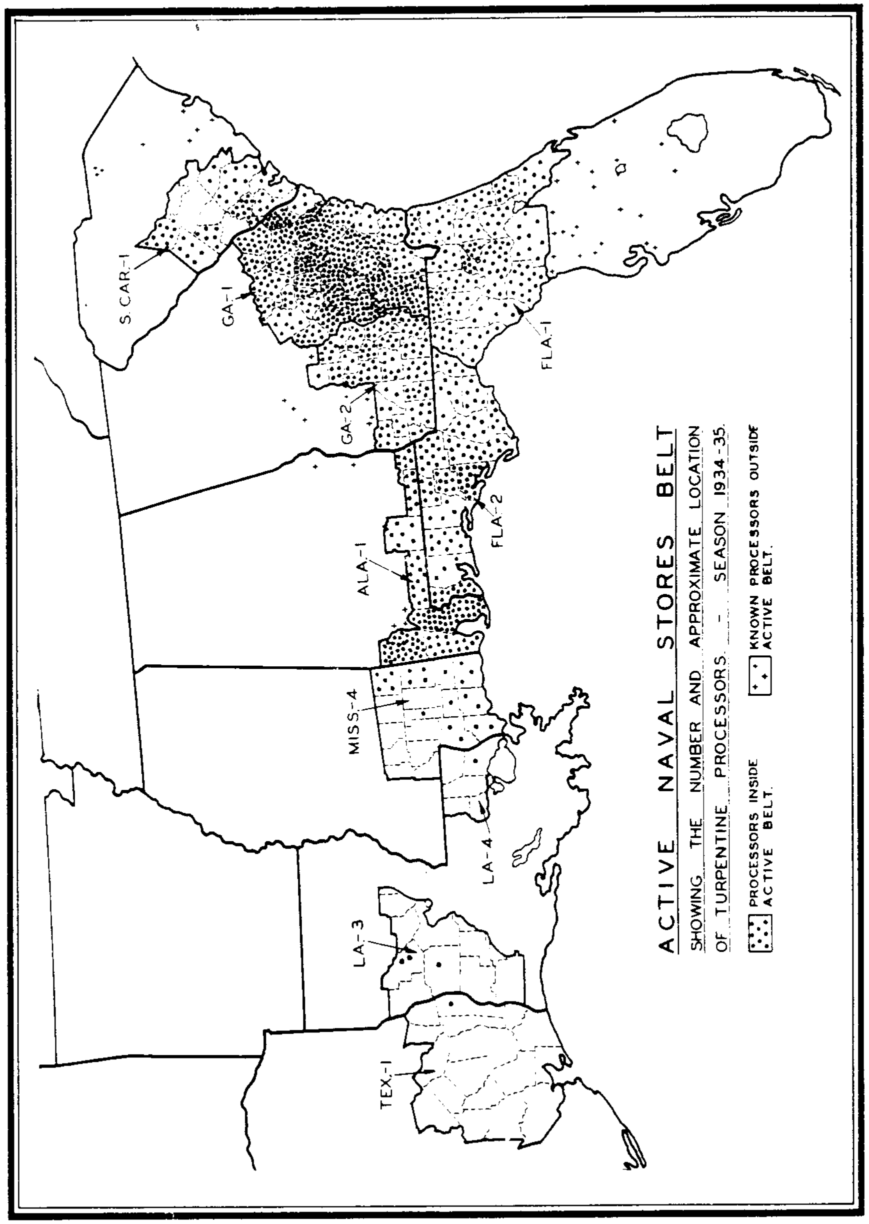

FIGURE 11. The distribution of the naval stores industry in the southeastern Atlantic and Gulf Coastal Plain, 1934–1935 (U.S. Forest Service 1935).

Early Uses of Sand Pine Scrub

In the early 1900s, sand pine was not highly valued as a timber-producing tree (Brown 1909). Firewood and fuel for steam engines of early trains were the biggest consumers of wood from these forests. The Flagler Railroad, completed to Miami in 1896, needed large supplies of fuelwood from local sources that were stacked along the tracks by contracted cutters. Large volumes of timber were removed adjacent to the railroad, much of which was slash pine that grew on the Miami rock ridge (Richardson 1977). As these cheap fuels were exhausted, the railroads converted to coal or diesel engines.

The well-drained soils of sand pine sites were converted extensively to citrus and pineapple production (Rolfs 1901, Stubenrauch et al. 1914, Austin et al. 1977). Most site conversions occurred on the east coast dune sites and the scattered inland relict dune sites south of Marion County. These coastal scrubs were destroyed for production of pineapples and citrus; typical site preparation involved total removal of large trees and shrubs followed by burning of slash piles. Next, plowing uprooted the remaining native vegetation. Finally, these sites were raked clean prior to planting of the fruiting crops (Rolfs 1901).

The largest scrub area, now contained in the Ocala National Forest, was not impacted greatly by this fruit production because technology did not exist for such immense site conversion. Overall, sand pine scrub forests were not severely impacted by early agricultural conversion. Scattered scrub "islands," however, probably were eliminated by small-scale farming.

Well-drained scrubs were prized not only for special crops but also for homesites. As was the case for use of south Florida slash pine forests, better transportation networks that penetrated southern Florida encouraged immigration by people from northern states. Upland sites were developed because large-scale drainage systems had not been created; thus scrubs and rocky pinelands were the first areas cleared for urbanization. Since these areas were considered wastelands, no one was concerned about scrub losses. Klopatek et al. (1979) showed that 14.8% of the original sand pine scrub remained based on 1967 land-use data.

With increased populations in southern Florida, changes in natural fire regimes led to decadent scrub (Austin et al. 1977). Cutover lands were burned frequently in an effort to clear the land for grazing or agriculture, which did not allow natural reseeding of sand pine. Many of these scrub sites today are classified as scrubby flatwoods (Richardson 1977). These changes in natural fire patterns also occurred in the Big Scrub of Ocala National Forest. Natural fire breaks between longleaf pine islands and scrub were reduced or eliminated following the harvest of longleaf pine, which allowed more frequent invasions of fire into the scrub (Webber 1935). Lumbering and turpentining activities within the longleaf pine forests of the Ocala area were more important in causing this shift of fire occurrence than was urbanization.

Modern Uses of Sand Pine Scrub Forests

Today, sand pine forests are actively managed only within the Ocala National Forest. The pulpwood potential of sand pine was realized in the 1930s and current industrial management practices are structured around pulpwood production (Cooper et al. 1959). Typically, scrub forests are clearcut and the newly cut sites are intensively site prepared. Reseeding is necessary because the serotinous cones do not open sufficiently after cutting operations to allow for natural regeneration. Oaks and other shrub species resprout following site preparation. Nonetheless, these scrubs are less diverse than natural stands because understory plants are reduced by site preparation and the dense, closed canopy of sand pine.

Scrub sites outside the Ocala National Forest tend to be small and disjunct; little protective management is feasible (Myers 1990). Continued population growth in Florida has resulted in rapid conversion of scrub forests to homesites and shopping malls (Fernald 1989). Austin et al. (1977) stated that the only preserve in southeast Florida large enough to contain healthy scrub was Jonathan Dickinson State Park in southern Martin County. The impacts of these losses remain unknown; these sites serve as important recharge areas for aquifers because of the well-drained nature of scrub soils. Loss of more recharge areas will further compound the water problems of south Florida. Sand pine scrubs of the southern Lake Wales Ridge continue to be converted to citrus production (Christman and Judd 1990; I. J. Stout, personal observation) in spite of the fact that the region is a center of endemism with numerous federally listed species of plants and animals. Chemical pesticides applied in the groves (e.g., ethylene dibromide—EDB) easily leach through the deep sands and can enter drinking water supplies (Kantrowitz 1989).

Use and Development of Subtropical Pine Forest

Subtropical pine forests were historically found along a "ridge" or outcrop of limestone that extended from Miami southwest about 88.4 km to Mahogany Hammock in Everglades National Park and were no more than 6.4 to 8 km across at the widest point. These pinelands also extended onto the Florida keys. This pine forest was a unique and relatively small component of the total pineland forest picture in the southeast.

This ridge was unsuitable for ranching because of the irregular surface with numerous solution holes (Harper 1927). Limited development for agriculture (fruits and vegetables) gave way to urban development; this has resulted in the complete removal of this pine woodland in the northeastern half of its range outside Everglades National Park. Only a few natural remnants remain of this forest type and they are almost exclusively within the park and the National Key Deer Refuge on Big Pine Key. Those remnants outside public ownership tend to be heavily invaded by exotic plants (Alexander and Crook 1974).

Conservation

Each of the pineland ecosystems discussed in this chapter contribute to the maintenance of local, regional, and continental biodiversity. A major goal of conservation biology today is the preservation of biodiversity (Norse et al. 1986, Wilson and Peter 1988). Threats to the pine forests of the southeastern U.S. take many forms but largely derive from the conversion of these natural systems to more intensive land uses such as plantation forestry, agriculture, and urban development. This development scenario, repeated at various spatial scales and rates throughout the region, inevitably results in reduction in size of natural areas and an increase in their fragmentation and isolation within the landscape (Wilcove et al. 1986 and reference therein). Those pinelands that do remain in public or private holdings often undergo undesirable ecological change because historic natural disturbance regimes are absent altogether or changed in terms of frequency or timing of occurrence (Means and Grow 1985, Jackson et al. 1986, Stout et al. 1988). Each pineland ecosystem type shares these problems and additionally poses other management challenges that are idiosyncratic.

The longleaf pine–wiregrass ecosystem has been highlighted as an endangered ecosystem (Means and Grow 1985, Noss 1989). It has been estimated that the original ecosystem may have occupied between 24 and 35 million ha; about 2 million ha remain and much of this land is mismanaged (Means and Grow 1985, Jackson et al. 1986). Management for old growth (e.g., greater than 70 years old) longleaf pine is critical to the long-term survival of the red-cockaded woodpecker on national forests (Jackson et al. 1986). Other species and biotic diversity in general will benefit from concerted efforts to maintain the red-cockaded woodpecker on national forest lands as required by the National Forest Management Act of 1976 (Norse et al. 1986).

Preservation of the fauna of the rockland pinelands depends on proper management of this habitat type within public lands associated with Everglades National Park and the Big Cypress National Preserve (Patterson and Robertson 1981, Dalrymple 1988). The most critically endangered animal associated with but by no means restricted to these pinelands is the Florida panther (Belden 1988/1989).

The conservation of longleaf pine–turkey oak sandhills throughout their distribution in the Gulf and Atlantic Coastal Plain and sand pine scrub and scrubby flatwoods in Florida depends heavily on immediate land acquisition programs. As noted by Frost et al. (1986), Myers (1990), and Ware et al. (Chapter 10 in this volume), very little of these ecosystem types remain in public ownership. Furthermore, maintenance of the conservation values depends on future and more detailed understanding of the use of fire to maintain the biota along the resource and spatial gradients represented in the region.

ECOLOGICAL RESEARCH AND MANAGEMENT OPPORTUNITIES

This chapter has broadly defined five pineland communities of Florida and the lower Coastal Plain. Regardless of their classification, these pinelands share a series of external threats to their long-term integrity, experience local and regional impacts of another spate of anthropogenic influences, and yet remain only generally understood in terms of landscape structure and function. The categories of major threats include (1) continuing conversion of these communities for pine plantations, agriculture, and urban use; (2) establishment of exotic species; (3) community fragmentation; (4) air pollution; and (5) overall loss of biodiversity. How then should research be planned to accommodate these regional problems?

Inventory of remnant pineland communities is a primary concern in view of mounting development pressures in the Atlantic and Gulf Coast region. Each state needs a Natural Area Inventory as conducted in North Carolina, Georgia, and Florida under the auspices of The Nature Conservancy. Minimal informational needs include (1) community type, (2) location, (3) ownership, (4) area, (5) resource condition, and (6) management status. Communities in most danger of loss within the region could then be focused on for land acquisition. Likewise, local research consortia could undertake study of these systems as well as the more ubiquitous ones.

Research on the pinelands needs to be organized around cogent questions directed at landscape, ecosystem, community, and population levels of complexity and carried out by multidisciplinary teams (Likens 1985). Categories of research needs may be identified with attributes of community structure, function, and management (Table 13). Basic information is lacking on species composition of the pineland communities. The flora is generally better known than the fauna, of which vertebrates are more completely catalogued than the more numerous invertebrates (Corey and Taylor 1989, Deyrup 1989). Species interactions (competition, predation, commensalism, mutualism, etc.) are poorly understood. A notable exception is the gopher tortoise and its burrow commensals in the better drained pinelands (Woodruff 1982, Jackson and Milstrey 1989). A general paucity of data exists with respect to functional attributes of pinelands. Even a general food web based on quantitative data has not been described for these pinelands. Nutrient cycling studies conducted in these systems are seldom reported in the literature (Howell et al. 1975, Croom 1978) or are limited to highly managed systems (Gholz et al. 1985). Early manipulations of pinelands with prescribed burning was prompted by landowners willing to finance research on bobwhite quail. Management of pinelands involves very little other than prescribed burning even today. Long-term research on the effects of fire management on the pineland biota is badly needed. Management of pine plantations is more intense and seeks generally to maximize yield of wood products as opposed to other natural resources.

TABLE 13 Research Needs of Pinelands of the Southeastern Atlantic and Gulf Coastal Plain Based on Data Available in the Published Literature[a]

	Structural Attributes			Functional Attributes			
	Species Composition						
Community Phases	Flora	Fauna	Species Interactions	Productivity	Energy Flow	Nutrient Cycling	Management and Manipulation
Pine flatwoods							
Longleaf pine	F	G	P	F	P	P	F
Slash pine	G	G	P	G	P	F	F
Pond pine	F	P	P	P	P	P	P
Rockland pinelands	G	F	P	P	P	F	F
Sandhills	F	F	P	P	P	P	F
Sand pine scrub	G	F	F	P	P	P	P
Scrubby flatwoods	F	F	P	P	P	P	P

[a] Informational categories relate to structure, function, management, and experimental manipulation (pulse, push protocols). Availability of information within each cell has been evaluated and classified as poor (P), fair (F), or good (G). Research needs are most acute in the cells classified as (P).

Development pressure has fostered a need to conduct research on how much landscape is necessary in some state of protection to conserve natural communities. One approach is to identify keystone species within each community, determine the size of minimum viable populations, and their area requirements (Stout et al. 1988). Very little research with these objectives has been done in the pinelands and it has great potential to assist in preserve design.

Pinelands exist within a landscape mosaic of other natural communities. The important ecological connections between and among these communities remains poorly documented (Noss and Harris 1986). Emphasis on protection and preservation of examples of particular communities may be of limited value without natural linkages to other landscape units. Research on these patch-corridor connections should be encouraged (Stout and Corey 1990).

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10

Southern Mixed Hardwood Forest: The Former Longleaf Pine Forest

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Editors' Note: The Resource Use and Management Effects section is placed in the early part of this chapter because the historically dominant vegetation and the forest products produced on the Coastal Plain were entirely different from composition and use of a Southern Mixed Forest recognized by Küchler (1964) and others for the same region.

INTRODUCTION

Perhaps 95% or more of the upland forests of the southeastern Atlantic and Gulf Coastal Plains have pine as a dominant of important component in the canopy. Once longleaf pine (*Pinus palustris*) was the most abundant species, with slash pine (*P. elliotii*) next most abundant; now both are greatly outnumbered by loblolly pine (*P. taeda*). Authors emphasizing past vegetation, present prevailing vegetation, or preferred timber management procedures have mapped the region as Longleaf Pine Forest (Sargent 1880), Southeastern Pine Forest (Shantz and Zon 1924), Southeastern Evergreen Forest (Braun 1950), or Longleaf–Slash Pine Forest and Loblolly–Shortleaf Pine Forest (the latter at the western, northern, and northeastern margins of the region) (U.S. Geological Survey 1970). In contrast, writers who emphasize the potential natural upland vegetation when fire is excluded name the region on the basis of the hardwoods that might ultimately dominate. They have considered the (potential) upland forests of the region as part of the oak–hickory association (Oosting 1956), as a beech–magnolia association