

# Arthropods Associated with Xeric Longleaf Pine Habitats in the Southeastern United States: A Brief Overview

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## ABSTRACT

The arthropods of xeric longleaf pine habitats in the southeastern United States are poorly known. Conservatively, between 4000 and 5000 species are characteristic. Perhaps ten percent of these are endemic types, many of which are related to taxa characteristic of xeric habitats of the Southwest. Arthropod herbivores and litter detritivores in this system seem to have important roles related to community function. Because over seventy percent of the flowering plants are entomophilous, pollination processes may also have significant effects on the community. Disturbance factors, including reduction of natural fire frequency, forestry practices, and the introduction of exotic species may have major effects on arthropod diversity and abundance. Increased knowledge of the arthropod fauna is needed in order to understand, protect, and manage these systems.

## INTRODUCTION

In this paper, we present an overview of the current knowledge of arthropods in xeric longleaf pine (*Pinus palustris*) habitats. The data is sparse and to attempt a thorough coverage of arthropods at this point is futile. Here we merely attempt to summarize pertinent literature and speculate on topics of significance.

The arthropods associated with longleaf pine habitats are poorly known. Wharton (1978) noted a paucity of information about the fauna of longleaf sandhill sites. The dearth of information is not surprising since most of the arthropod faunas of the continent are little studied. Unfortunately, the arthropod fauna may have already been affected by anthropogenic changes to the extent that determining its characteristics under "natural conditions" may be difficult.

We are limiting the scope of this overview in several ways. 1) We consider only sandhill and dry savanna habitats, not the full range of longleaf pine sites. 2) Geographically, our comments pertain largely to the Coastal Plain of the southeastern United States, east of the Mississippi River.

Habitats west of the Mississippi River are significantly different from those in the east (Peet and Allard this volume, Harcombe et al this volume). *Pinus palustris* communities above the Fall Line in Alabama and Georgia are floristically very different from those on the Coastal Plain. The arthropod fauna above the Fall Line and in the western part of the range may also be quite different. 3) Only free-living, terrestrial taxa are included in this paper. We have excluded groups of arthropods with aquatic immature stages, although dragonflies, for instance, may be common in longleaf pine habitats. Nor have we considered the specialized parasitic insect orders in which all species use animal hosts as adults, i. e., the Siphonaptera (fleas), Mallophaga (biting lice), and Anoplura (sucking lice). Of the groups considered, most species, perhaps 90%, also occur in various other habitats.

The characteristic arthropod fauna of dry longleaf pine habitats in the southeastern United States probably includes a minimum of four thousand to five thousand species. We base this very conservative estimate on literature sources (most of which are not included in the literature cited in the interest of space conservation) using pitfall trap, light trap, and sweepnet samples, and on general

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collecting done over the past twenty years (Deyrup, unpubl., Folkerts unpubl.). A fauna of this size is probably small compared with, for instance, the number of species found in eastern deciduous forest habitats. Longleaf pine habitats subjected to frequent fires are probably more correctly viewed as woodlands, characterized by relatively low structural complexity and correspondingly low faunal diversity. Nevertheless, in species richness, arthropods greatly exceed all other animal groups in longleaf pine systems. This diversity seems to guarantee that arthropods have an important and complex role in the functioning of this system.

Part of the information presented here has resulted from our own investigative efforts. Much is based on a compilation of knowledge amassed by previous workers. Our literature citations include only the few necessary to document statements or to assist the reader in acquiring further information. They are by no means comprehensive or complete. If no citations are noted, the statements reflect information gathered by or opinions of the authors.

We view our tasks in this paper to be: (1) a preliminary aggregation of the relatively scant and scattered information that exists in the literature, combined with the occasional extrapolation of information from other systems to the longleaf pine system, (2) a presentation of preliminary results of our own work, and general impressions gained from our familiarity with the system, (3) the generation of hypotheses, and (4) an attempt to draw attention to some of the more conspicuous gaps in our knowledge. We hope that our speculations will encourage formulation of more explicit hypotheses.

## **XERIC LONGLEAF PINE HABITATS FROM AN ARTHROPOD PERSPECTIVE**

Before considering specifics of the arthropod fauna, we briefly characterize the habitat as it might appear from the viewpoint of arthropods.

The soil is usually excessively drained, infertile, and sandy, with little humus or clay. This creates problems for species that lose moisture easily, particularly because sand abrades the thin covering of wax that protects arthropods from desiccation. Burrow construction is a problem because burrows need constant maintenance, rainwater percolates through the burrows, and the coarse soil

structure allows predators easy access to the inhabitants. On the other hand, for species that tolerate desiccation, the ease of burrowing in the sandy soil can be advantageous. It allows root feeders to graze easily on the dispersed roots of plants. It allows predators to search broadly for prey without excessive energy expenditures. Ground-nesting species can excavate elaborate galleries that seldom flood for more than a few hours. The ease of vertical movement in the soil allows inhabitants to locate optimum conditions of temperature and humidity.

In frequently burned sites the litter is reduced to a thin layer of needles and leaves and the luxuriant arthropod fauna associated with deep litter layers seems almost absent. However, microsites with accumulated litter remain in abandoned tortoise burrows and burned out stumpholes. In some areas, clumps of oaks may shade out the fire-carrying wiregrass and litter may accumulate. All in all, although the list of litter-inhabiting arthropods may be quite long, their ecological role is likely to be minimal because where fire is frequent they are confined to microsites.

A habitat with an overstory of scattered large pines with a few small trees and shrubs in the understory does not seem conducive to the development of a diverse assemblage of insects. The open nature of the canopy may expose arthropods to extremes of weather and to easy detection by predators. However, the diversity is surprising. Pine foliage supports some polyphagous arthropods and a surprisingly rich fauna occurs under the loose outer layers of pine bark. Additional diversity occurs in small areas of distinctive habitat, as with the litter fauna. Dead twigs and branches are invaded by a succession of bark and wood feeders and the occasional dead pine may attract a great variety of species. Cavity-nesting vertebrates provide habitat for a diverse array of commensals and parasites. Oaks that have survived fire harbor a diverse phytophagous fauna quite different from that found on pine. The arthropod fauna associated with herbaceous species is poorly known.

In a dense broadleaf forest much of the arthropod activity takes place in the canopy, the habitat below the canopy being primarily the domain of decomposers. However, in xeric longleaf pine stands the ground vegetation receives most of the sunlight and even the surface of the soil is exposed to high light intensity and air movement. Many arthropods are dependent on these conditions and disappear or emigrate if the habitat becomes shaded. This is even true of species of ants and

digger wasps that are not directly dependent on open-site plants.

The herb layer is often sparse. A number of the plants are sclerophyllous, making feeding difficult or requiring long feeding periods. These conditions may expose herbivores to predators; consequently, many herbivorous species may be cryptic, distasteful, evasive, or tough-bodied. Recently burned sites, because of the burst of new plant growth, offer herbivores optimal conditions if they can persist through fires or recolonize such sites.

## CHARACTERISTIC SPECIES: A BRIEF SURVEY OF THE GROUPS

In this section, species that are characteristic or unusual are highlighted. We include crustaceans, myriapods, arachnids, and insects, the latter comprising the bulk of the fauna. Members of all insect orders except the Grylloblattodea may be found in longleaf pine habitats. Other species are covered in the sections on longleaf pine herbivores and on species associated with the gopher tortoise and the southeastern pocket gopher.

When common names are used, the binomen is included only the first time the species is mentioned. In general, common names, ordinal names, and the scheme of classification follow Stoetzel (1989). The term "pest" is often applied to phytophagous arthropods in the literature of forest entomology. This term has meaning only from a limited anthropocentric viewpoint and will not be used in this paper.

### Crustacea

None of the burrowing crayfishes occur in xeric longleaf pine habitats, although several species are common in pitcher plant bogs and are occasionally found in wet flatwoods. The terrestrial isopods (sowbugs, pillbugs) are also largely restricted to moister sites. However the anthropophilic *Armadillium vulgare*, an introduction from Europe, is found in longleaf pine habitats and may be common in trash piles and garbage dumps (Folkerts pers. obs.). Native species such as *Ocelloscia floridana* can occasionally be found in pockets of moist litter, such as partially filled gopher tortoise burrows.

### Arachnida

Spiders are the most conspicuous arachnids in longleaf pine habitats, but in both numbers of species and numbers of individuals, mites (Acari) greatly exceed the spiders. Most mites, however, are so small that they escape notice. Many mite species are associated with litter or soil. A number parasitize vertebrates or live in their nests or dens. A large number of arthropods, especially among the Coleoptera and Hymenoptera, have associated mites. Most others are found on the surfaces of plants, several species often being encountered in flowers. Some parasitize animals. To most visitors to longleaf pine habitats, the only mite ever consciously encountered is the chigger, *Eutrombicula alfreddugesi*. Mites are mentioned again later in the section on litter decomposition.

Among the wind scorpions (Solifugae), the only southeastern species, *Ammotrechella stimpsoni*, is occasional in longleaf pine habitats in Florida, although it is more abundant in other habitats in the southern portion of the peninsula (Muma 1967).

The giant whip scorpion or vinegaroon, *Mastigoproctus giganteus* (Uropygida), is still relatively common in some areas of peninsular Florida. In the southeastern U.S. it is mainly a denizen of sandhill habitats. Individuals are active at night. During the day they take refuge in burrows, holes, or under logs.

In Florida, the scorpions *Centruroides hentzi* and *Vejois carolinianus* (Scorpiones) are commonly encountered in longleaf pine habitats. The latter species is the common scorpion in similar areas north of Florida. Neither has venom dangerous to humans.

A number of species of harvestmen (Opiliones) may be encountered in longleaf pine habitats. *Leiobunum uxorium* is often found crawling on the surfaces of trees.

Pseudoscorpions (Pseudoscorpiones) are poorly studied as a group and are not well known in the southeastern U.S.; many species are undescribed. A number occur in longleaf pine habitats. They are found in forest floor litter, under bark, in the nests of mammals and birds, and in association with ants and termites. Pseudoscorpions are key members of the community of flattened arthropods that inhabit the loose outer bark

of longleaf and slash pines (Brach 1979). One type, seemingly a species of *Garyops* (Sternophoridae), is commonly encountered under the bark of dead pines where it preys on other arthropods. Corey and Taylor (1987) reported on the scorpions, pseudoscorpions, and harvestmen of flatwoods sites in central Florida, but xeric sites have not been studied. Muchmore (1990) provided a key to pseudo-scorpions associated with soil.

At least 50 species of spiders (Araneae) are commonly encountered in longleaf pine systems. The largest and most obvious orb weaver, *Argiope florida* (Araneidae), is essentially restricted to sandhill and dry pine savanna habitats. It makes a large web at heights of about 2m. In habitats where bare sand is present, burrowing wolf spiders of the genus *Geolycosa* (Lycosidae) are often common. Among the more abundant species are *G. patellonigra*, *G. turricola*, *G. ornatipes*, and *G. pikei*. *Geolycosa xera*, McCrone's burrowing wolf spider, inhabits both sandhill and scrub habitats and has been considered threatened in Florida (Edwards 1982). Wallace (1942) and McCrone (1963) dealt with the taxonomy of the genus *Geolycosa*. The numbers of *Geolycosa* at most sites appear to have declined in the past two decades (see section on disturbance). The threatened rosemary wolf spider, *Lycosa ericeticola* (Lycosidae), is known only from a small area in north-central peninsular Florida. It occurs in longleaf pine habitats in which rosemary (*Ceratiola ericoides*) is abundant (Wallace 1982, Reiskind 1987). Throughout much of the Southeast, the northern widow, *Latrodectus variolus* (Theridiidae), is the common widow spider of longleaf pine habitats although it does not range into peninsular Florida where the black widow, *L. mactans* occurs. The red widow, *L. bishopi*, is more common in scrub habitats but may be found in sandhill sites in peninsular Florida. Another theridiid, *Steatoda fulva* characteristically constructs webs above the entrance to harvester ant nests (Hölldobler 1971b). The trapdoor spider, *Myrmekiaphila fluvialis* (Ctenizidae), occurs in sandhills and dry pine savannas. This nominal species may be a complex of species including forms with different habitat preferences (N. Platnick, pers. comm.). Muma (1973) recorded several spider species from flatwoods sites. Some of these also occur in more xeric habitats.

## Myriapods

The myriapods include the four arthropod classes Chilopoda (millipedes), Diplopoda (centipedes), Pauropoda (pauropods), and Symphyla

(symphylans). None of these taxa is well known in the southeastern U.S..

*Scolopendra viridis* seems to be the most common large centipede in longleaf pine habitats. It occurs in decaying logs and in relatively deep pine litter. Shelley (1987) reported this species from sandhill sites in North Carolina.

Hoffman (1990) noted that acid soils and pine litter harbor few species of millipedes, so perhaps we should expect few in longleaf pine habitats. However, he did note that polyxenids may occur in pine litter in great numbers. These small millipedes seem to be adapted to drier sites than are many other millipede taxa and are often encountered in longleaf pine habitats, especially under loose bark flakes on large pines.

Sheller (1990) indicated that pauropods occur mainly in deciduous litter and that they are not common in dry sites. Hence, this group also may be poorly represented in longleaf pine habitats.

Among the samples of symphylans examined by Edwards (1958) the lowest numbers were found in sands and clays. This may suggest that symphylans are not abundant in longleaf pine habitats, but no information exists.

## Insecta

**Protura.** These primitive, wingless hexapods typically inhabit organic litter and soil. They are occasionally encountered in Berlese samples from longleaf pine habitats but we have not identified any to species. DuRant and Fox (1966) found proturans to be relatively abundant in litter under loblolly and shortleaf pines in the Piedmont of South Carolina.

**Thysanura.** Among the silverfish, most species are associated with human habitations. The only species usually encountered in longleaf pine habitats is the widespread *Allocrotelsa spinulata* (Lepismatidae). Wygodzinsky (1972) reported it from a number of sites characterized by sandy soils. It is found under bark and objects.

**Archaeognatha.** Although we have observed jumping bristletails in longleaf pine habitats, we do not know their identity. Ramsey (1941) recorded *Machilis variabilis* (Machilidae) from beneath the bark of *Pinus echinata* and *P. taeda* in North Carolina.

**Diplura.** These small insects, usually 3-5mm in length, are abundant in leaf litter and soil. Two or three species have been found in Berlese samples from longleaf pine habitats. The common species are members of the families Campodeidae and Japygidae.

**Collembola.** Springtails are common inhabitants of forest floor litter throughout the world, but they tend to be most abundant in habitats cooler and moister than dry longleaf forests (DuRant and Fox 1966, Christiansen 1990). The dry sparse litter present at sites that burn frequently seems to provide little habitat for most species. At sites where litter has accumulated, a moderate springtail fauna is found in Berlese samples. Species encountered are mainly members of the Entomobryidae, with some Isotomidae, Sminthuridae, and Onychiuridae also represented. Some entomobryids, whose bodies are protected from desiccation by a layer of surface scales, are very common in soil and on bark in xeric longleaf pine stands.

**Orthoptera.** The large American grasshopper *Schistocerca americana* is common in longleaf pine habitats throughout the southeastern U.S.. Its ecology has been studied by Kuitert and Connin (1952). Wharton (1978) noted adults congregating in sandhill habitats during the winter. The eastern lubber grasshopper *Romalea guttata* is the largest grasshopper occurring in longleaf pine habitats. In contrast to other species, the aposematic nymphs feed in groups after hatching in the spring. Among the other characteristic acridids are *Amblytropidea occidentalis* (Shelford 1963) and a group of flightless *Melanoplus* species, several of which are restricted to sandhill habitats. Among the tettigoniids, *Arethaea phalangium*, *Orchelimum minor*, and *Conocephalus saltans* have been said to be typical (Shelford 1963). Several species of flightless crickets, including two species of bar-faced ground crickets (*Pictonemobius* sp.) (Gross et al. 1989), the two-toothed scaly cricket (*Cycloptilum bidens*) (Love and Walker 1979), and Hebard's bush cricket (*Falcicula hebardii*) (Blatchley 1920), are essentially restricted to longleaf pine-wiregrass habitats.

**Blattodea.** Shelford (1963) found the small yellow cockroach *Cariblatta lutea* to be characteristic of sandhill habitats. Dakin and Hays (1970) indicated that it is often seen on low vegetation at night. *Arenivaga floridensis*, the Florida sand cockroach, burrows in sand and may be found under surface litter; it is restricted to Florida. Hubbell and Goff (1939) said that the cockroach *Parcoblatta fulvescens* was common in longleaf pine habitats. *Eurycotis floridana*, called the stinking cockroach

because it may emit an odoriferous liquid, is the largest cockroach of longleaf pine habitats, some individuals reaching lengths of more than 30 mm. It is encountered beneath litter and under loose bark, and is frequently anthropophilic. All individuals are wingless.

**Mantodea.** The mantid *Thesprotia graminis* is characteristic of pine forests in the southeastern U.S. The wingless female resembles a dead pine needle. *Brunneria borealis* and *Stagnomantis carolina* also occur but are more common in moister habitats.

**Phasmatodea.** The slender-bodied walking-stick *Manomera tenuescens* occurs in longleaf pine habitats from North Carolina to Florida. Specimens have been collected on wiregrass (*Aristida stricta* or *A. beyrichiana*). The related *Manomera brachypyga* occurs in similar habitats, but is restricted to Florida.

**Dermaptera.** Shelford (1963) noted that *Prolabia pulchella*, one of our few native earwigs, was frequently encountered in sandhill habitats. It is commonly found under bark.

**Embiidina.** Several species of webspinners occur in the southeastern U.S. but we have not encountered any in longleaf pine habitats. However, there seems to be no reason why they should not be present.

**Isoptera.** Three termite species, all belonging to the genus *Reticulitermes*, the subterranean termites, occur in xeric longleaf pine habitats. *Reticulitermes flavipes* seems to be more common than are *R. virginicus* or *R. hageni*, but there are many sites where all three species occur. Their relative abundance seems to vary geographically. Rhinotermitids are encountered most frequently in fallen logs, but may be found in standing snags to a height of five or six meters. They are important decomposers (see below).

**Psocoptera.** Psocids are common in longleaf pine habitats on vegetation and among the litter. García Aldrete (1990) listed 35 species of psocopterans that may occur in litter in the southeastern U.S. Mockford (1974) reported both *Echmepteryx hageni* and *E. youngi* (Lepidopsocidae) from the foliage of longleaf pine and sand live oak (*Quercus geminata*) in Florida and Georgia. *Archipsocus nomas* (Pseudocaeciliidae), a species that makes visible webs on trees, is occasionally seen. Psocids are often small scale scavengers, functioning like minuscule cockroaches.

**Zoraptera.** The only zorapteran occurring in the southeastern U.S. is *Zorotypus hubbardi* (Zorotypidae). These small, pale, colonial insects are found in rotting wood, in sawdust, and in association with termite colonies. This species is encountered occasionally in longleaf pine habitats.

**Thysanoptera.** These small insects are abundant in most habitats and many species occur in longleaf pine sites. Most species feed on plants and may be common in flowers, especially Asteraceae. Fungus-feeding species are commonest in leaf litter but occur in other habitats as well. A few species prey on other arthropods. Occasionally, individuals will bite humans but do not imbibe blood.

**Heteroptera.** Adults and nymphs of the common coreid *Chelinidea vittiger* are often abundant on the surface of *Opuntia humifusa*, their only host in longleaf pine forests. During the winter, adults hibernate on the underside of the cactus pads (Baranowski and Slater 1986). The lygaeid *Oncopeltis fasciatus*, called the large milkweed bug, is often abundant on the flowers and fruits of species of *Asclepias* and *Matalea pubiflora*. Several other species of *Oncopeltis* may be locally common. The cryptic stink bug, *Brochymena carolinensis* (Pentatomidae), often rests on the bark of longleaf pine. A common red and black assassin bug, *Apiomeris spissipes* (Reduviidae), attacks bees and wasps on flowers or lies in wait by harvester ant nests.

**Homoptera.** This order contains numerous species of aphids, leafhoppers, cicadas, and scale insects, which are abundant in xeric longleaf pine habitats. All feed by sucking plant juices and a number are important vectors of plant diseases. Unfortunately, little specific information is available. Some species are mentioned in the section on arthropods of longleaf pine.

**Neuroptera.** The funnel-shaped pitfall traps of ant lions (Myrmeleontidae) are often seen in sandhill habitats. There are several species, the most widespread being *Myrmeleon carolinus*. Lewis and Stange (1981) provided a key to the Florida *Myrmeleon*. Ant lions of the genus *Brachynemurus* do not build pitfalls but lie in wait for prey beneath the sand surface. The species *B. carolinus*, *B. pumilus*, and *B. ramburi* inhabit sandy soils in the Southeast (Stange 1970). Certain species of green lacewings (Chrysopidae) and brown lacewings (Hemerobiidae) spend their entire lives in the crowns of pine trees where their larvae feed on aphids and other herbivorous insects.

**Mecoptera.** Larval scorpionflies are usually associated with moist humic soil and are therefore not likely to be common in xeric sites. *Panorpa lugubris* (Panorpidae) and *Bittacus pilicornis* (Bittacidae) are frequently seen resting on vegetation in longleaf pine habitats.

**Lepidoptera.** Based on the general literature, we estimate that at least 400 species of butterflies and moths occur in sandhill and dry longleaf pine savanna habitats. This is probably a gross underestimation because more than a thousand species belonging to this order have been taken at light traps at the Archbold Biological Station in Highlands County, Florida.

Shelford (1963) reported that the buckeye butterfly, *Junonia coenia* (Nymphalidae) breeds in sandhill habitats, where its major larval host plants are species of *Aureolaria* (Scrophulariaceae). Adults of this species are among the most commonly sighted butterflies. Larvae of the zebra swallowtail butterfly *Eurytides marcellus* (Papilionidae) feed on plants of the genus *Asimina*, several species of which occur in longleaf pine habitats. *Yucca flaccida*, and *Y. aloifolia* (Agavaceae), the former being more common, are the larval host plants for the giant yucca skipper, *Megathymus yuccae* (Hesperiidae). The Cofaqui skipper, *Megathymus cofaqui* also occurs on yucca, but has a more restricted distribution (Opler and Krizek 1984). Caterpillars of the palmetto skipper, *Euphyes palatka*, construct tube-like shelters at the bases of leaves of saw palmetto, *Serenoa repens* (Arecaceae). The larva of the fiery skipper, *Hylephila phyleus*, feeds on grasses (Poaceae) in sandhill areas (Watson 1926).

Yucca flowers may harbor one to several individuals of the yucca moth, *Tegeticula yuccasella* (Incurvariidae), the only insect capable of pollinating yuccas in the Southeast. Larvae inhabit yucca fruits which often show evidence of conspicuous exit holes later in the season.

Other common butterflies include various sulfurs (Pieridae) (*Eurema* spp., *Phoebis sennae*), hairstreaks (Lycaenidae) (*Calycopis cercrops*, *Eurystrymon favonius*, *Satyrium calanus*, *Strymon* spp.) and blues (Lycaenidae) (*Hemiargus* spp.). Flower moths of the genus *Schinia* (Noctuidae) may commonly be found resting on flowers. The leaf mines of microlepidoptera, such as *Stilba* sp., are often abundant on turkey oak leaves (Faeth and Simberloff 1981).

**Coleoptera.** The beetles are a large, extensively studied group of insects in the southeastern U.S.,

although still very incompletely known. At least 700 species occur in xeric longleaf pine habitats.

Many beetles spend at least part of their life cycle in the soil and are thus sensitive to soil conditions. A number of species are adapted to the unique soil conditions found in xeric longleaf pine habitats. These species are seldom found elsewhere except perhaps in sand pine scrub or coastal dune habitats. This habitat specificity is most conspicuous in the families Cebrenidae, Cicindelidae, Scarabaeidae and Tenebrionidae, although there are probably additional examples among the Alleculidae, Carabidae, Elateridae, and Staphylinidae. The five southeastern species of the scarab genus *Mycotrupes* provide a good example of species confined to southeastern xeric uplands (Howden 1964). Adults construct burrows, sometimes as deep as eight feet, which are obvious because of the conspicuous piles of heaped up sand at the entrances. Larvae in the burrows feed on provisions of dung gathered by the parents (Woodruff 1973). A commonly seen predaceous beetle is the metallic blue tiger beetle, *Cicindela unicolor*, which seems to be restricted to dry longleaf pine habitats. Larvae inhabit burrows in the soil.

The metallic blue chrysomelid *Hemispherota cyanea* feeds on the leaves of saw palmetto *Serenoa repens* (Arecaceae). The conspicuous larvae cover themselves with filamentous masses of frass. This species is uncommon in the driest habitats, where the host plant is rare.

*Strepsiptera*. During their larval stages, these unusual insects parasitize other insects, usually Hymenoptera or Homoptera. Adult males of unidentified species are sometimes found at light traps in longleaf pine habitats.

*Diptera*. At least 450 species of flies occur in drier longleaf pine habitats, but almost nothing is known about the fauna. Fly diversity tends to be greatest in moist habitats. In xeric pinelands species are often associated with moist microhabitats such as carrion, feces, fleshy fungi, fleshy fruits, sap fluxes, and vertebrate burrows. A few species with larvae that actively burrow in the soil are restricted to sandy uplands.

The crane fly *Tipula oxytona* (Tipulidae) is unique to longleaf pine forests. Adult females oviposit in the sand at the edge of wiregrass clumps and the larvae feed on wiregrass rootlets (Rogers 1933). A number of robber flies (Asilidae), bee flies (Bombyliidae), mydas flies (Mydidae), and stiletto flies (Therevidae) have soil-dwelling larvae and are

among the most conspicuous flies in upland longleaf pine habitats.

*Hymenoptera*. Xeric longleaf sites probably support hundreds of species of this large order. Ants are conspicuous, including subterranean species that never come to the surface, arboreal species that never enter the soil, and many species that nest in the soil and forage above ground. In contrast to the relative paucity of knowledge on most of the arthropods of the longleaf pine system, the eastern harvester ant *Pogonomyrmex badius* is relatively well known (Carlson and Gentry 1973, Golley and Gentry 1964, Gordon 1983, 1984a, b, Hangartner et al. 1970, Harrison and Gentry 1981, Hölldobler 1971a, b, Hölldobler and Wilson 1970, Porter 1986, Wilson 1958). The species is the only member of its genus in eastern North America. Many other species occur west of the Mississippi River, mainly in desert areas of the southwest (Cole 1968). Its large conspicuous mounds make it the most obvious ant in dry longleaf pine habitats. It does not occur at sites lacking areas of open sand.

Wharton (1978), citing a personal communication from J. B. Gentry, indicated that the common ants in sandhill habitats in Georgia are *Crematogaster punctulata*, *Pheidole dentata*, *Solenopsis (Diplorhoptrum)* sp., and *Pogonomyrmex badius*. In North Carolina, Carter (1962) found that xeric longleaf pine stands were characterized by the ants *Aphaenogaster treatae*, *A. lamellidens*, *A. floridana*, *Camponotus socius*, *Crematogaster lineolata*, *C. ashmeadi*, *C. minutissima*, *Forelius pruinosis*, *Formica shaufussi*, *Leptothorax texanus*, *Pheidole morrissi*, *P. dentata*, *P. metallescens*, and *Trachymyrmex septentrionalis*. Appendix I is a list of ants known from dry longleaf pine habitats in Florida.

The various gall wasps of the family Cynipidae form a bewildering array of galls on various parts of oak trees (Weld 1959). Nearly thirty species may attack bluejack oak (*Quercus incana*). As many as twenty-five species may be found on turkey oak (*Q. laevis*). Sand post oak (*Q. margaretta*) may harbor fifteen species. A common and conspicuous species, *Amphibolips cinerea*, forms groups of large spherical leaf galls at the terminal ends of branches of bluejack oak.

## Arthropods Associated with Gopher Tortoises and Pocket Gophers

The gopher tortoise *Gopherus polyphemus* and the southeastern pocket gopher *Geomys pinetus*, excavate permanent burrows in sandy habitats in the southeastern U.S. The existence of these under-

ground chambers coupled with the presence of dung produced by the animals has evidently presented an unusual evolutionary opportunity for a number of arthropod lineages in the southeastern U.S. Several associates have developed adaptations to subterranean conditions, including depigmentation, elongate appendages, and reduction in eye size. A number of the species are obligate inquilines and are not known from other habitats. In the literature, these have often been called commensals. However, even casual associates could have commensal relationships with the hosts. The term "commensalism" does not necessarily imply that the association is obligate.

Papers by Young and Goff (1939), Woodruff (1973, 1982a, b), Milstrey (1986), and Lago (1991) included information on arthropods found in the burrows of the gopher tortoise (cf. Appendix II). Sixteen of the species seem to be obligate associates. The large number of obligate species suggests that adaptation to the specialized resources of tortoise, tortoise dung, and burrow conditions may have evolved over a relatively long period. The obligate species include one pseudoscorpion, one harvestman, one cave cricket, three flies, two moths, and eight beetles. Many other arthropods are occasional or regular associates. One, *Ceuthophilus latibuli*, a cave cricket, also occurs in pocket gopher burrows, but none of the obligate species occur with both vertebrates.

The gopher tortoise is declining in numbers, largely because of habitat destruction and alteration, and human depredation (Auffenberg and Franz 1982, Diemer 1986). Populations west of the Mobile-Tombigbee rivers are protected as threatened under the Endangered Species Act. However, none of the arthropods associated with the tortoise is federally protected, although some species have been placed on the candidate list. Some have been listed as declining or rare in Florida (Woodruff 1973a). Lago (1991), after examining 246 burrows at 48 localities, found fewer of the obligate species in Mississippi than have been reported from areas in Florida, where the tortoise is more abundant. Whether this is the result of a decline in tortoise numbers or is characteristic of more peripheral northern populations cannot be ascertained. Programs in which gopher tortoises are removed from sites where the habitat is being destroyed and relocated to sites where they will presumably survive do not involve relocation of arthropods. Thus, populations of the tortoise which may be offered the most protection may not afford protection to the burrow associates.

The arthropod associates of the southeastern pocket gopher have been studied by Hubbell and Goff (1939), and some were mentioned by Woodruff (1973, 1982b) (cf. Appendix III). We are not aware of any recent thorough studies. Sixteen of the species are probably obligate associates, including two centipedes, one spider, one silverfish, one springtail, two cave crickets, one moth, one fly, and seven beetles. A number of other species may be present in varying degrees of frequency. Several obligate associates have been listed as declining or rare in Florida (Woodruff 1982b). In 1988, we excavated pocket gopher burrows in the Fall Line sandhills of Russell County, Alabama, where this mammal apparently has declined markedly in the last three decades. Few arthropods were encountered, and only one was possibly an obligate associate known from sites investigated in Florida by Young and Goff (1939). Here again, it is difficult to determine if the apparently depauperate arthropod fauna at this site is the result of the decline in pocket gopher populations or has always been the case in these peripheral populations at the northern extremity of the range of the host. Some isolated populations of pocket gophers may have been separated from core populations for long periods. Although the southeastern pocket gopher can survive in disturbed areas such as roadsides and fields, the species, along with its arthropod associates, may be declining in many parts of its range, not just on the fringes.

It is likely that a number of the species associated with both vertebrate hosts are yet to be described. A moth associated with the gopher tortoise was discovered as recently as 1988 (Davis and Milstrey 1988). S. W. Bullington and A. F. Beck are describing a new asilid fly that seems to be an obligate inhabitant of gopher tortoise burrows. Recently, an apparently undescribed pholcid spider was collected from a gopher tortoise burrow in central Georgia (D. and G. Folkerts, unpubl.). Additional research may reveal unforeseen relationships. For example, Skelley (1991) found that the scarab beetle *Stephanucha thoracica* depends on patches of decomposing vegetation killed by burial under pocket gopher mounds.

The food webs in which the arthropod associates of these two vertebrates are involved are based largely on the feces of the host. None of the intricacies of the ecological interactions among the species have been worked out. It is not known how the obligate inquilines locate new burrows, an especially perplexing problem with the flightless forms. It is possible that some are phoretic on the

vertebrate hosts. Even were this so, it cannot explain how flightless tortoise associates colonize burrows made by a young tortoise that has never been in contact with an adult. Because the hosts occupy island-like habitats, the habitat of the associates could be thought of as an island within an island. Studies on these topics must be done soon before further loss of localized arthropod associates occurs.

## AFFINITIES AND AGE OF THE FAUNA

The biogeography of arthropods of xeric longleaf pine habitats is complex. Fragmentary evidence suggests many types of endemism, speciation, and differentiation, but we lack the detailed information necessary to piece this information together to form a coherent picture. The deficiency in our knowledge is the result of several factors. 1) We lack adequate distributional data for many species and with the present rate of habitat destruction, may never be able to obtain it (Deyrup 1990). 2) To erect logical hypotheses on faunal origins, the phylogenetic history of the groups in question must be adequately known. This information is generally lacking. Three decades ago, Gressitt (1958) felt that our knowledge of insect zoogeography was "imperfect and uneven." Little progress has been made since. 3) The biogeographic history of the longleaf pine plant community is complicated and any discussion of related faunal origins must be very general.

Because of the excessively drained sandy soil and the open nature of the habitat, it is not surprising that the fauna of xeric longleaf habitats shows a general resemblance to those of sand pine scrub habitats and even coastal dune habitats. There are fewer similarities to the fauna of longleaf flatwoods and little resemblance to the fauna of the wettest habitats such as pitcher plant savannas. Similarities among the faunas of sandy uplands do not necessarily provide information about the origins of the species involved. Highly vagile species may be able to colonize all available habitat, thus obscuring their origins. For example, the eastern harvester ant *Pogonomyrmex badius* is widely distributed in sandy uplands. However, until there has been a more detailed analysis of the differences among populations, the pattern reveals nothing about biogeographical relationships among isolated upland regions.

On a larger scale, certain patterns seem to be present. The eastern harvester ant is the sole eastern representative of a genus whose center of radiation is southwestern North America (Cole 1968). This pattern, linking the xeric uplands of the Southeast and arid areas of the Southwest is found repeatedly. In some cases eastern and western populations are similar enough to be considered a single species, as with the desert snapping ant (*Odontomachus clarus*) (Deyrup 1990), the vinegaroon, and the scrub jay (*Aphelocoma coerulescens*). The assumption that these lineages originated in the western portion of the continent is supported by patterns in which one or two southeastern species appear to be derived from a diverse group of western congeners. This pattern is found in sand roaches of the genus *Arenivaga* (Hebard 1920), mydid flies of the genus *Nemomydas* (Kondratieff and Welch 1990), and the vertebrate genera *Aphelocoma*, *Cnemidophorus*, *Gopherus* (*sensu lato*), and *Sceloporus*. The geotrupine scarab genera *Bradycinetulus* and *Eucanthus* may be additional examples (Howden 1955, 1963, Woodruff 1973). These patterns may support the idea of a trans-austral subtropical savanna corridor in the early Pleistocene (Webb and Wilkins 1984). Determining whether eastern or western taxa are ancestral may present problems. Even so, groups that are speciose in the western portion of the continent, and have only one or a few eastern representatives, probably originated in the west.

In addition to widely distributed species, xeric upland habitats also harbor a number of narrowly restricted endemic species. The apterous scarab genus *Mycotrupes*, for example, has five apparently allopatric species in isolated areas of sandy habitat (Woodruff 1973). Another scarab genus, *Phyllophaga*, includes a number of species known only from a few sandhill localities (Woodruff and Beck 1989). The beetle genus *Selonodon* (Cabrionidae) appears to have a number of narrowly restricted species in sandy areas, although little information is available on habitats and distribution (Galley 1990). The grasshopper genus *Melanoplus* (Acrididae) includes a large number of taxa unique to the southeastern uplands (Hubbell 1932, 1961).

These examples have been fortuitously discovered during taxonomic studies. If systematic sampling of longleaf pine uplands were to be done, numerous other patterns of endemism would probably be found. Available information is insufficient to allow us to make any definitive statements about

relationships between isolated or semi-isolated areas. This data is not only necessary to understand biogeographic patterns but is critical in making decisions about protection of the biotic diversity of the Southeast.

The age of the taxa confined to xeric longleaf habitats cannot be reliably estimated. Fossil pollen profiles are interpreted differently by different workers. It is possible that the dominance of longleaf pine has occurred for the past 5,000 years (Watts 1971), or for as long as 18,000 years (Delcourt and Delcourt 1985). The most recent information (Watts pers. comm.) shows alternating periods of domination by oaks and pines going back almost 40,000 years. The arthropod fauna was undoubtedly affected by these fluctuations. Fall Line sandhills supporting longleaf pine and associated biota, may have been available since the Cretaceous (Duke 1961). This suggests that many of the taxa may have originated before the genesis of upland longleaf pine habitats.

## ARTHROPOD INFLUENCES ON COMMUNITY STRUCTURE AND FUNCTION

### Introduction

Arthropods are likely to have a significant influence on community structure and function in longleaf pine habitats, but their effects have not been quantified. Arthropods function in many ways including filling rolls as: 1) herbivores, 2) soil modifiers through soil tillage, 3) mediators of decomposition, 4) pollinators, 5) vectors of plant and animal diseases, 6) dispersal agents of plant propagules, 7) predators and parasitoids of other arthropods, and 8) prey. The conceptual model shown in Fig. 1 depicts the major ways in which the activities of arthropods affect longleaf pine systems.

### Herbivory

It is unlikely that many plant species escape arthropod herbivores. Crawley (1983), considering all ecosystems, thought that 33 percent of all animal species were herbivores and indicated that an average of 10 percent of the primary productivity of natural ecosystems is taken by herbivores of all kinds. Chew (1974) said that herbivores take less than 20 percent. Whatever the value, arthropods consume a sizable fraction of the plant biomass. The percentage of herbivorous types in the arthro-

pod fauna of xeric longleaf pine habitats is unknown, but we estimate it is between 30 and 40 percent.

Regarding the regulation of plant populations, opinions range from a belief that herbivory regulates ecosystem function (Chew 1974, Mattson and Addy 1975) to the opinion that it has little or no function in plant population dynamics (Hairston et al. 1960). It might be expected that herbivores would always depress plant productivity and perhaps regulate plant populations, but there is disagreement on these topics. In some cases, grazing by insects results in increased foliar output and a concomitant increase in net primary production (Owen 1980). Mattson and Addy (1975) indicated that defoliating insects may consume up to 40 percent of the plant foliage in an area without reducing plant growth.

We know essentially nothing about palatability or defensive mechanisms for most of the plant species in longleaf pine habitats. Often, plants of poor soils have low tissue moisture levels, are highly lignified, and contain high concentrations of secondary metabolites (Mattson 1980). Bracken, *Pteridium aquilinum*, a common plant of longleaf pine habitats, is known to possess cyanogenic glycosides, but the percentage of plants possessing the compounds varies (Cooper-Driver and Swain 1976). The herbivores of this species have been thoroughly studied at a number of sites in its worldwide range (Lawton 1976, 1982, 1984). A similar study in the southeastern U.S. would yield interesting comparative information.

Herbivores may limit the habitat distribution of plant species within an area (Parker and Root 1981). Similarly, the extent of the geographic range could be affected by herbivory. This may occur most frequently at the periphery of ranges where other factors weaken plants (see below).

In some cases, herbivory can be regarded as a method by which components of plant tissues are rapidly cycled back to the soil and ultimately to the plants. Feces formed by herbivores usually become components of the soil or litter. Webb (1976) considered insect feces to be merely a prepulverized form of litter that offers greater surface area for microbial colonization. Defoliation of trees by herbivores has been found to increase soil nitrogen levels (Bocock 1963). Mortality resulting from attack by herbivorous arthropods may be a mechanism by which materials are cycled from weak to healthy trees. Schowalter et al. (1981) contended that the southern pine beetle was important in

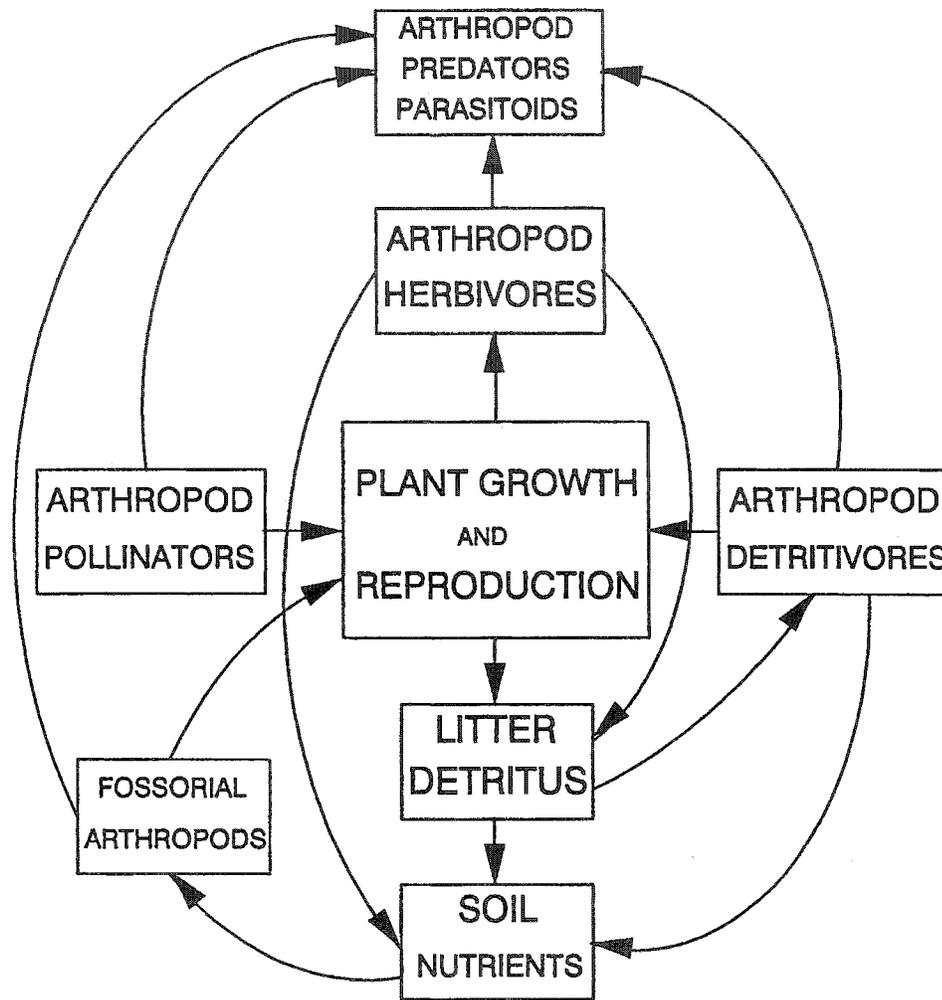


Figure 1. Conceptual model showing the ways in which arthropods are hypothesized to function in xeric longleaf pine habitats. The arrows represent effects and linkages, not energy flow, materials flow, or food web phenomena.

maintenance of community structure and function in southeastern pine forests. They felt that high diversity and productivity were the result of the production of patches of fire-susceptible dead trees by this species.

There have been very few studies of the herbivorous arthropods of longleaf pine communities. Faeth and Simberloff (1981) studied the effects of experimental isolation on the leaf-mining insects of three southeastern oak species, including *Quercus hemispherica*, a plant often found in dry longleaf pine habitats, although it seems to be a penetrant that is most abundant in the absence of fire.

Severe defoliation events seem to be exceptionally rare in xeric longleaf pine systems. In 1989, the leaf area removed from turkey oaks by adult buprestid beetles (*Brachys ovatus*) was measured at a site in Toombs County, Georgia. Nearly five per-

cent of the leaf area was removed (n= six trees, Folkerts unpubl.). Outbreaks such as this, in which each tree was attacked by hundreds of beetles, are rare. In Florida sandhills, lupines (*Lupinus* spp.) and gopher apples (*Licania michauxii*) are often heavily attacked by caterpillars, but the infested plants persist and bloom.

### Herbivores of longleaf pine

Longleaf pine is well-known as an arthropod-resistant species (cf. Wahlenberg 1946); most arthropods inflict minimal damage most of the time. Appendix IV contains a list of 42 arthropod species to attack longleaf pine trees within the native range of the species, a relatively short list for a North American pine. In part, the brevity results from forest entomologists concentrating on species with the potential for causing economic damage. There are probably additional generalized herbi-

vores that cause minimal damage. Even so, other species of *Pinus* in the southeastern U.S. support considerably more herbivores. For instance, more than 50 species are known to attack loblolly pine (*Pinus taeda*). Longleaf pine seems to have evolved mechanisms to prevent attack by species that, in other pines, are considered by foresters to be exceptionally damaging. The southern pine beetle, *Dendroctonus frontalis* (Scolytidae), is unable to invade the bark of healthy longleaf pines, but can decimate stands of other species. The Nantucket pine tip moth *Rhyacionia frustrana* (Tortricidae) often heavily infests nearly all two- and three-needle pines but does not attack longleaf pine or slash pine (*Pinus elliotii*).

Among the insects that do attack unweakened longleaf pine trees, many are much more common on other hosts, indicating a degree of resistance in longleaf pine. Some families of insect herbivores are entirely absent from longleaf pine. Gagne (1989) listed no plant-feeding gall midges (Cecidomyiidae) that infest longleaf pine, and we know of only two species that occasionally occur. Species of this family are known to attack at least 18 other *Pinus* species in North America, including *P. echinata*, *P. elliotii*, and *P. taeda*. Even outside its native range, longleaf pine is notably resistant to attack by arthropod herbivores. Of 26 native and exotic pines studied in a botanical garden in California, longleaf pine was the most resistant to attack by the sequoia pitch moth, *Synathedon sequoiae* (Sesiidae) (Weidmann and Robbins 1947).

The remarkable resistance of longleaf pine to attack by herbivorous arthropods is thought to be related to its ability to mobilize high volumes of resin at the site of an attack (Hodges et al. 1979). In addition to the physical barrier provided by the resin, its effectiveness may be related to the toxicity of monoterpene vapors produced (Smith 1965). The major monoterpenes in *P. palustris* are alpha-pinene and beta-pinene (Mirov 1961). Total flow, flow rate, viscosity, and time to crystallization of the resin are all related to resistance (Barbosa and Wagner 1989). Evidently, the ability of invading insects to induce resin crystallization and thus successfully invade the tree is low for longleaf pine. Geographic differences in resin characteristics, known in other *Pinus* species (Smith 1977), are undocumented in longleaf pine. Franklin and Snyder (1971) found individual but no regional differences in alpha- and beta-pinene among longleaf pines sampled in Florida, Mississippi, and Louisiana. They thought that oleoresin composition was under relatively strong genetic control.

Among the few insects which attack healthy *P. palustris* trees, three seem to affect its reproductive success most markedly. Longleaf pine is the preferred host of the longleaf pine seedworm *Cydia ingens* (Tortricidae). The larvae of this moth devour the internal portions of the seed, destroying up to 21 percent of the seed crop in some years (Baker 1972). Older nymphs and adults of the leaf-footed pine seed bug *Leptoglossus corculus* (Coreidae), may cause heavy seed loss in longleaf pine (DeBarr 1967). In other pines, the loss may be 100 percent because of conelet abortion resulting from the feeding of small nymphs. The southern pine coneworm *Dioryctria amatella* (Pyralidae) may cause heavy cone losses. The life cycle of this insect is complex and many parts of the tree may be attacked (Coulson and Franklin 1970). Low cone production in some years may reduce the impact of seed and cone herbivores by decimating their populations to levels too low to limit seed yield in years of heavy cone production.

However, once a longleaf pine is weakened or dies, invasion by a host of arthropods is possible. There may be a relatively orderly sequence to this invasion. Numerous phloeophagous and xylophagous herbivores attack weakened trees. Many predators, parasitoids, fungus-feeders and other associates follow. Three years after death, a standing longleaf pine may harbor several hundred arthropod species.

### Soil movement by arthropods

Fossorial arthropods and species that construct burrows of some type during at least a part of their life cycle are conspicuous components of xeric longleaf pine habitats. Among the most evident types are the eastern harvester ant *Pogonomyrmex badius*, ants of the genus *Pheidole*, geotrupine scarab beetles, and a number of ground-nesting wasps and bees. There are well over one hundred species whose activities result in the movement of soil.

The significance of soil movement by arthropods has not been thoroughly studied in any North American habitat, and very little information exists about its possible ecological role in longleaf pine systems. Because earthworms are not abundant in xeric longleaf pine habitats, fossorial arthropods may play a more important role than they do in moister habitats (Barbosa and Wagner 1989). Murphy (1955) contended that soil movement by ants may substitute for the activities of earthworms in systems where the latter are not abundant. Kalisz and Stone (1984) found that the scarabaeid *Peltotrupes youngi* was responsible for

significant amounts of soil mixing in a Florida sandhill site. In an attempt to measure the volume of soil moved by arthropods at a sandhill site in Washington County, Florida, we collected all soil in one ha that had been moved by *Pogonomyrmex* and *Pheidole* ants and scarab beetles. This totaled approximately 0.8 m<sup>3</sup> for the hectare. It should be noted that this sample was biased; the site was chosen because of abundant evidence of burrowing arthropods.

Soil movement by arthropods could conceivably produce a number of effects. First, nutrients leached to lower levels in the soil may be brought to the surface where they may be more available to plants. Second, nudation by spreading subsurface soil over the surface may provide germination sites and/or safe sites for the growth of some plant species. Third, aeration and percolation of water through the soil via burrows may be of significance. This last factor is less likely to be important in porous sandy soils. Fourth, organic material may be introduced into the soil.

Translocation of materials from lower layers of the soil by earthworms can increase surface nutrient amounts significantly (Satchell 1967, Lofty 1974). However, soil movement by arthropods in xeric longleaf pine systems may not have this effect. Gentry and Stiritz (1972), examined soils in harvester ant habitat that had not been disturbed by the ants. They found phosphorus amounts to be greater on the surface of the soil than beneath the surface, and found potassium amounts to be about the same. Under these conditions, transport of soil to the surface could not result in surface nutrient increase, at least for these nutrients. Leaching may carry nutrients to levels below which the burrows of most arthropods reach.

There is also little to support the idea that soil brought to the surface by arthropods may provide germination sites or safe sites for some plants. The enhanced growth of grasses and forbs found near harvester ant mounds by Golley and Gentry (1964) was attributed to nutrients brought in the form of seeds harvested by the ants rather than to nutrients brought up from below the soil surface.

Historically, nudation and translocation of nutrients to the surface may have been brought about mainly through the burrowing activities of gopher tortoises and pocket gophers which burrow deeply and bring up large volumes of material (Kaczor and Hartnett 1990).

## Litter arthropods and their function

Arthropods are abundant and diverse in the litter of all forests and woodlands. As far as we can determine, no methodical studies have been done in xeric longleaf pine habitats. In other habitats, arthropods can accelerate or delay the release of nutrients from decomposing organic matter (Crossley 1976). Madge (1965) found that tropical forest litter generally decomposed more slowly when arthropods were excluded. The roles played by litter arthropods in xeric longleaf pine habitats have not been studied. Worldwide, arthropods in litter have a number of important functions. Their direct actions involve grazing on the litter itself or on microflora growing on the litter. They may be important in litter comminution, i.e., the breakdown of large fragments into smaller ones. Comminution results in increased available surface area for colonization by the microflora. Colonization of pine litter by fungi and bacteria may be impossible without rupture of the needle cuticle by arthropods. Grazing on the microflora may be important in regulating the population growth of fungal and bacterial components and thus may affect the rate of litter breakdown. During this process, dispersal of bacteria and fungal spores may occur. Movement of arthropods through the litter may mix litter materials. Arthropods, often species different from those which graze on the microflora, may ingest portions of plant litter (Harding and Stuttard 1974). Predatory arthropods in the litter may affect the mycophagous and detritivorous forms, indirectly influencing the rate of litter breakdown.

In longleaf pine habitats litter is composed of pine needles, leaves of woody angiosperms, herbaceous plant parts, twigs and branches, bark fragments, components of fallen trees, cones, fruits, flowers, and seeds. Minor components may include animal feces and exudates, and materials arriving via dryfall and stemflow. We have sampled the litter fauna by Berlese techniques at a few sandhill and dry longleaf pine savanna sites in southern Alabama and south-central Georgia. Mites, ants, springtails, fly larvae, beetles, and termites were the groups most abundant. Mites were numerically the most abundant group. However, beetles tend to be the most diverse in most litter systems (Barbosa and Wagner 1989). Millipedes, which Webb (1976) found to be a dominant group in deciduous forests, were not abundant in our few samples. Crossley (1976) indicated that mites and collembolans were important in litter breakdown. Termites of the genus *Reticulitermes* are often very abundant, although few species are represented.

Jeanne and Davidson (1984) said that termites are of greater ecological importance than their relatively low species richness might suggest. We believe that termites are important decomposers in xeric longleaf pine areas because they move easily through the sandy soil and take advantage of surface wood by extending their tunnels into dead branches and tree trunks. This behavior allows them to take advantage of accumulations of cellulose with minimal exposure to drying conditions and fire.

Meentemeyer (1978) indicated that litter decomposition rates increase from north to south in eastern North America. This conclusion was probably based on the fact that temperature means and length of the warm season generally increase in such a pattern, as does rainfall. However, this generalization may not apply to drier longleaf pine sites. In contrast to other habitats, leaf and needle litter is not fragmented and mixed into lower layers within a year. There may be several reasons for the seemingly slower breakdown rates. First, the xeric nature of the sites is likely to retard litter breakdown. Arid conditions are known to limit the activities of decomposing organisms (Swift et al. 1979). Most arthropods cannot ingest dry freshly fallen litter (Harding and Stuttard 1974). Second, polyphenolic compounds manufactured by plants are produced in highest amounts on acid, nutrient-poor soils, typical of these habitats. These substances may inhibit fungal and faunal activity (Swift et al. 1979). Third, pine needles, cones, and bark litter are more resistant to decomposition than are the products of broad-leaved trees (Barbosa and Wagner 1989).

Arthropods may be more important in litter processes and materials cycling in xeric longleaf pine habitats than in deciduous forests because earthworms seem rare in these habitats. Most coniferous litter cannot be handled by earthworms. In absolute terms, however, arthropods may be relatively unimportant in litter decomposition in habitats in which frequent fires consume much of the litter. We mention the litter fauna in the later section on fire.

## Pollinators

Worldwide, arthropods (mainly insects) are the most important animal pollinators of plants. Various native bees, especially bumblebees and megachilids, are frequent flower visitors in longleaf pine habitats. Flies, especially syrphids and bombyliids, also visit many herbaceous species.

For at least a century, students of pollination have been interested in community-level phenomena beyond the mere relationship of plant and pollinator (Robertson 1895). In most communities, the majority of pollinating insects are polylectic, obtaining pollen and nectar resources from a number of plant species. This is the case with pollinating insects that interact with the flora of longleaf pine habitats. A few oligolectic species occur, such as the anthophorid bee *Habropoda laboriosa*, which restricts most of its activities to various *Vaccinium* species, and the megachilid *Lithurge gibbosus* which collects pollen only from *Opuntia*. There is one monolectic species, the incurvariid moth *Tegeticula yuccasella*, the ethnodynamic pollinator of *Yucca flaccida*.

We have constructed a pollination spectrum for the plants of an abstract longleaf pine community in the central Gulf Coast region (Fig. 2). This is based on 317 plant species that have been noted as characteristic of xeric longleaf pine habitats in various literature sources. Almost 75% (231 species) are entomophilous based on flower structure and/or observations. Of the remaining species, 62 (19.5%), mainly trees and graminoids, are clearly wind pollinated. One species (0.3%), *Satureja*

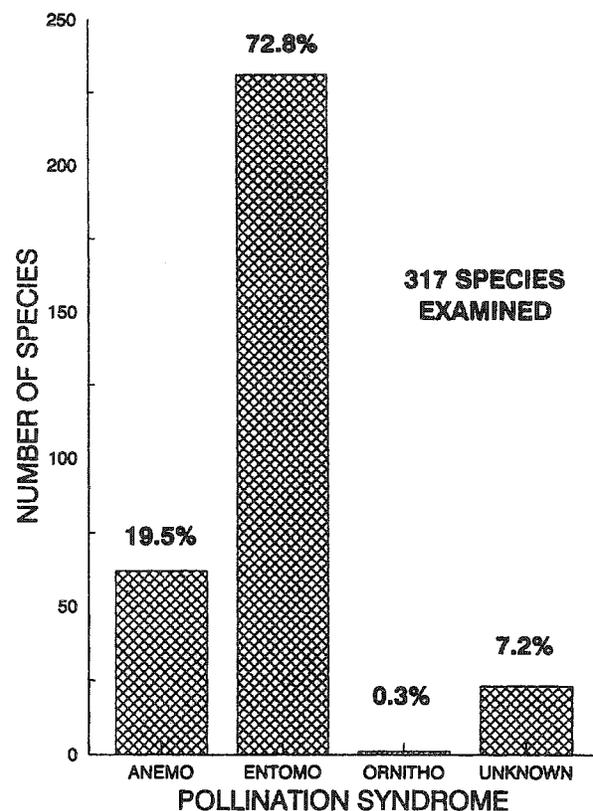


Figure 2. Pollination spectrum of the flora of xeric longleaf pine habitats. ANEMO = Anemophily, ENTOMO = Entomophily, ORNITHO = Ornithophily.

*coccinea* (Lamiaceae), has features suggesting ornithophily by hummingbirds. The ruby-throated hummingbird (*Archilochus colubris*) frequently visits this plant (Folkerts, unpubl.). The pollination system of the remaining 23 (7.2%) species is unknown, but some are entomophilous.

Because the bulk of the flora is entomophilous, it can be posited that insect pollinators have significant effects on the community. Most of the pollinators interact with a number of plant species. Therefore, the totality of their influence on the community is probably complex. Competition for pollinators may occur in some communities (Mosquin 1971) and could affect reproductive success of the various plants and/or community structure. Competition for pollinators has been hypothesized to result in evolutionary changes in flowering time (Anderson and Schelfhout 1980). Platt et al. (1988) stated that regularly spaced flowering phenologies in longleaf pine forests "are not a consequence of selection for divergence in flowering time resulting from competition for pollinators." However, we feel that stimulation of flowering by fire does not rule out pollinator competition as a factor in determining flowering time. Clearly, many plants of moister longleaf pine habitats are adapted to pollination by insects that are only present for short periods, e.g., large-flowered *Sarracenia* and queen *Bombus*.

### Dispersal of plants by arthropods

The dispersal of diaspores (seeds, fruits, and other reproductive structures) by terrestrial arthropods is essentially limited to cases of myrmecochory, dispersal by ants. In some habitats the seeds of more than 25 percent of the species are dispersed by ants (Beattie 1985). Myrmecochory has not been studied in longleaf pine habitats, but is a common phenomenon in the eastern deciduous forest of North America, where the seeds of many common spring-flowering herbs are dispersed by ants (Handel et al. 1981). It is possible that a small component of the flora of longleaf pine habitats is myrmecochorous. Likely candidates are species of *Polygala* (Polygalaceae). Most bear arils that may function as elaiosomes, structures containing high concentrations of nutrients that are removed from the seed and consumed by ants after the seeds are collected. Some *Carex* spp. and *Scleria* spp. (Cyperaceae) may be dispersed by ants. Certain members of these genera have outgrowths or projections on the achene or perigynium which may function as elaiosomes. Some of the

carunculate species of *Euphorbia* (Euphorbiaceae) may also be myrmecochorous.

Some dispersal may occur fortuitously as a result of the collection, transport, and subsequent loss of seeds without elaiosomes by ants that normally destroy the seeds. *Pogonomyrmex badius* and species of *Pheidole*, common ants in sandhill habitats, may be involved. Harvester ants drag longleaf pine seeds that have fallen on their mounds to peripheral sites away from the mound. Evidently the seeds of longleaf pine are not among their food items.

Berg (1975) stated that myrmecochores are common in communities where fire is frequent, but this does not seem to be the case in xeric longleaf pine habitats. It is possible that seeds stored in ant nests are at depths that prevent them from being destroyed by fire but still allow them to germinate eventually. However, cache sites are not always favorable germination sites. A seedling flora has not been reported to be associated with ant mounds in these habitats, but observations have been few. In other habitats, significant associations between ant nests and certain plant species have been found (Rissing 1986). It may be that dispersal of seeds from unburned sites to recently burned sites, where more favorable conditions for germination are present, is important for some species. However, many seeds may require heating by fire before germination will occur (Christensen and Kimber 1975). In this case, caching below the surface by ants would prevent germination and mere transport would not favor it. These phenomena should be explored.

### THE ROLE OF ARTHROPODS IN SUCCESSION

The possibility that herbivorous arthropods may play important roles in the direction and rate of plant succession has been suggested by a number of workers (Breedlove and Ehrlich 1968, 1972, Brown 1984). However, studies of succession in longleaf pine habitats have been dominated by those interested mainly in plants (e.g., Grelen 1962, Monk 1968, Peroni and Abrahamson 1986). There are no studies of plant-insect interactions during succession. Further complicating the picture is the fact that in habitats with frequent natural fires, successional phenomena are often not viewed as important because succession only occurs when fire is artificially suppressed.

Whatever one's view on succession, it is obvious that the vegetational state in longleaf pine habitats undergoes marked changes without fire. Even with frequent fires, species' abundance, vegetation pattern, and community longevity vary spatially and temporally. Investigations are needed to determine the extent to which these phenomena are affected by arthropods. There are a number of possible interactions between arthropods and successional phenomena in these habitats. Weakened trees are attacked by a variety of arthropod herbivores, often resulting in tree death that would not otherwise have occurred. It is possible that in the absence of fire, old longleaf pine trees are weakened by competition from invading vegetation and become susceptible to insect attack (Schowalter et al. 1981). Our experience suggests that older longleaf pines are more frequently attacked by bark beetles in areas where succession is advanced than in areas that have received frequent fire. Gaps created by eventual death of the tree provide areas for colonization by herbaceous plants, other tree species, or may release younger trees already present in the area.

Differential grazing by herbivores may mediate both intraspecific and interspecific competition among the plants in many habitats. McBrien et al. (1983) reported that grazing on goldenrods by a chrysomelid beetle had significant successional effects in an old field community in Ontario. The activities of fossorial arthropods may create safe microsites for seed germination and seedling growth. Both the destruction and dispersal of diaspores by arthropods could also have successional implications. Hobbs (1985) found that harvester ants (*Veromessor andrei*) had significant effects on plant distribution and abundance in California serpentine grassland. Foraging by the ant *Solenopsis geminata* has been shown to influence seed densities (Carroll and Risch 1984). (Further comments on the effects of ants may be found in the section on soil movement by arthropods.) Insect damage to fruits is known to influence their attractiveness to their normal dispersal agents (Manzur and Courtney 1984). Although not documented, many or all of these phenomena may occur in some form or other in xeric longleaf pine habitats.

## ARTHROPODS AND FIRE

If it can be assumed that arthropod diversity is in part a result of plant diversity because of the large number of arthropod herbivores and nectarivores in most habitats, then it is likely that frequent fires increase arthropod diversity in

longleaf pine habitats. In this forest type, frequent burning increases the biomass and species richness of herbs (e.g., Stoddard 1935, Hilmon and Hughes 1965, Hodgkins 1958, Gates and Tanner 1988).

Almost all of the studies on the response to fire of arthropods not found in soil or litter have involved collection by sweeping or vacuuming the herbaceous vegetation. Thus, many taxa may have been undersampled. In addition, most of the studies used winter rather than lightning-season burning, and only a few were based in longleaf pine habitats.

Hurst (1970) obtained more arthropods and more biomass from burned plots on a Mississippi power line right-of way than he did from unburned five-year-old plots. In contrast, Dunaway (1976) found more biomass and generally a greater abundance of arthropods on three-year-old "rough" than on annually burned sites in a longleaf pine forest in southern Mississippi. This may indicate that increases in arthropods after fire occur gradually until microhabitat diversity peaks, after which a decline begins. However greater numbers of individuals and greater dry weights of arthropods were found on strips and plots of *Koeleria cristata* in the area than in either of the pine areas. This suggests that arthropod abundance in the area was related to herbaceous biomass. Dunaway's results are difficult to interpret, however, because the area had historically been grazed by livestock, and grazing continued on his three-year-old plots during the study. His conclusions emphasize the importance of including the temporal aspects of burning when considering effects on the fauna. The greater abundance of arthropods three years postfire in his study may still have been a result of fire.

Harris and Whitcomb (1974), in Leon Co., Florida, found that six carabid beetle species were more abundant in litter without fire, but that two other species predominated on annually burned sites. To our knowledge, this is the only study dealing with arthropod response to fire at the species level.

Sisson (1991) sampled insect populations from areas subjected to either spring or winter burns in longleaf pine-wiregrass communities in southwestern Georgia. All sites were burned in the winter during the year before the study. During the study, half the sites were burned annually in late winter (February-March) and half in spring (April-May). Each site was sampled twice with 250 sweeps of a standard sweepnet through the ground cover veg-

etation. The study showed no significant differences in the numbers or volume of arthropods taken on areas burned in the spring versus areas burned in the winter (Sisson 1991).

The effects of fire on the arthropods associated with woody vegetation in longleaf pine habitats are poorly known. Other pine species, when weakened by fire, can be attacked by beetles that may not attack unweakened trees (Miller and Patterson 1927, Abrahamson 1984), presumably increasing local beetle diversity.

The effects of fire on the soil and litter fauna may be the reverse of fire effects on other arthropods. Although it is important to distinguish between the litter fauna and the soil fauna, few workers have clearly done so. It is likely that the fauna actually dwelling in the soil is less affected than that in the litter. Species that require bare sand benefit from fires. Heyward and Tissot (1936) found mites and collembolans to be far more abundant in longleaf areas that had burned infrequently than on sites with more frequent burns. Pearse (1943) obtained more chiggers (Trombiculidae) in samples from unburned sites than from burned sites in the Duke Forest, North Carolina.

Studies in other forests types yielded similar results. Buffington (1967) found fewer taxa and individuals one year after a wildfire in a pine stand in New Jersey. Metz and Farrier (1973), working in loblolly pine stands in South Carolina, established that mesofaunal arthropods were less abundant on annually burned areas than on control sites and areas burned less frequently than annually. Metz and Dindal (1975), working in the same area, found that numbers of springtails were greater on unburned and periodically burned plots than on annually burned plots. Species richness was greatest in periodically burned sites in several European studies (Forsslund 1951, Jahn and Schimitschek 1950, Huhta et al. 1967).

Immediate reduction of diversity and numbers following burning is the result of mortality of the litter fauna during combustion. Species inhabiting the mineral soil may not be drastically affected. In South Africa, Coult's (1945) claimed that most arthropods in the top inch of the soil survived ordinary burning. The reduction in species richness and numbers that continues for a time after burning seems to be due to the loss of microhabitats present in the litter, but may also be related to a reduction in the amount of food substrate. A result of the removal of longleaf litter by fire is a general reduction in soil moisture (Heyward 1939), which

also affects microhabitat suitability for much of the mesofauna. Additionally, changes in soil morphology may be related to reduction of arthropod numbers after fire. Heyward (1937) found that soils in annually burned longleaf pine plots showed greater morphological similarity to grassland soils than to forest soils.

Vegetational changes resulting from fire may alter the behavior of arthropod species. After a longleaf site was burned, eastern harvester ant foraging area increased and a greater number of individuals emerged from colony entrances per unit time (McCoy and Kaiser 1990).

Few studies on the effects of burning on arthropods have been detailed enough to obtain reliable data on species diversity. Ideally, future studies will incorporate the following:

1. Sampling of the fauna should be accomplished by several methods including sweeping or vacuuming, pitfall trapping, flight intercept (bumper, malaise) trapping, sticky trapping, and litter and soil sampling.

2. Sampling should be done at least monthly. The periodic nature of many arthropod life cycles means that significant data will be missed if the interval is longer. Preburn and immediate postburn samples should be included.

3. The vegetation should be sampled so that its condition can be correlated with the characteristics of the arthropod fauna. Information on flowering and fruiting phenologies is highly desirable. If the burn is patchy, extent and vegetative condition of the unburned patches should be recorded. Unburned patches should be sampled immediately after burning to determine their function as refugia and colonization nuclei.

4. Burning temperatures and intensity should be documented.

5. Measurements should be made of litter depth and composition, litter and soil moisture conditions, and soil type and profile.

6. Local climatological data should be noted.

## **ANTHROPOGENIC DISTURBANCE AND THE ARTHROPOD FAUNA**

Few, if any, sites exist where xeric longleaf pine habitats have not been modified by humans. In the

following section, we note possible effects of a number of types of human activity.

## Effects of forestry practices on arthropods

The ecological roles of forest insects, especially those associated with trees, are often in conflict with silvicultural goals. Many silvicultural activities create conditions that increase the likelihood that certain phytophagous arthropods will increase in number and impact. Included among these practices are: 1) creation of monocultures, 2) creation of uniform-aged stands, 3) production of abnormally high tree densities, 4) depression or eradication of other plant species, and 5) clearcutting (of large tracts).

Clearcutting has become the most common timber harvest practice in the southeastern U.S. Clearcutting itself, regardless of how the land is subsequently treated or restocked, has a number of effects on arthropod populations. The massive amounts of slash provide sites where phloeophagous and xylophagous insects can reproduce. This may result in unnaturally large populations that attack living trees in unusually high numbers. Machinery used in the clearcutting process often compacts the substrate. This may have immediate effects on the soil and litter arthropofauna. In addition, it almost undoubtedly creates conditions under which seedling establishment is more difficult. Seedlings weakened by the physiological stress associated with growth in compacted soil may be more susceptible to insect attack. The vegetation on the edges of clearcuts is often subjected to shock through physical damage by machinery and sudden exposure to higher light intensity. These factors would tend to increase plant susceptibility to attack by phytophagous arthropods. Continued nutrient removal by repeated harvest is likely to alter the site to the extent that a return to relatively natural conditions is unlikely for long periods, even if harvest ceases.

Site preparation most markedly affects the arthropods of the soil and litter. Disruption of arthropod activity in the litter layer may interfere with nutrient recycling. Site preparation usually mixes the litter with the soil. Under these conditions, litter breakdown may occur more slowly or more rapidly than normal, depending on soil type, moisture, and soil temperature. In any event, the arthropods present are only a remnant pauperized fauna. Site preparation also destroys the herba-

ceous and woody ground flora on which a significant component of the arthropod fauna depends. After site preparation significant floristic changes occur, among which is a decrease in wiregrass density. Weedy species characteristic of disturbed sites may become abundant (Abrahamson and Hartnett 1990). Possible consequences for arthropods are obvious. If stump removal is done, greater disturbance to the soil and vegetation, and thus to the arthropod fauna, occurs. Erosion is greater on site-prepared areas, especially if they are sloping. Nutrient loss associated with erosion may further alter the floristic composition and thus affect the insect fauna.

It is clear that the presence of numerous individuals of the same species of the same age in a dense stand creates conditions under which pathogens or herbivores can more easily attack large numbers of individuals (Schowalter et al. 1981). Seldom is resistance to phytophagous insects a component of "genetic improvement" programs for southern pines. The close spacing of trees in monocultures may weaken some to the extent that herbivore attack becomes more likely. Although a few plants of other species may survive as the trees in an even-aged stand grow, there are so few individuals and/or so few species that the ecological functions of a species rich system are absent. As an example, many hymenopterous parasitoids of phytophagous insects depend on nectar as a source of energy. In most monocultures, nectar producing plants are in low abundance and, because of shading, produce few or no flowers. The effect of parasitoids on populations of phytophagous species is thus negated.

A rarely mentioned factor that may be significant is that, under natural conditions, stands of other pine species were often fragmented by the widespread occurrence of the longleaf pine community. Dispersal of phytophagous insects inhabiting other pines may have been rare because of the barrier of the less susceptible longleaf pine. Insect outbreaks in stands of loblolly or slash pine could be considered anthropogenic events.

Monocultures are designed to be low in plant species richness. Because most of the arthropod fauna is associated with plants, arthropod species richness is unlikely to be high in these artificial habitats.

## Decline of a major predator

The red-cockaded woodpecker (*Picoides borea-*

lis) was once an exceptionally common insectivorous bird throughout most longleaf pine habitats in the southeastern United States. Habitat destruction and alteration have reduced populations to the extent that the species is now federally protected as endangered. In general, all associated insectivorous bird species tend to decline when xeric longleaf pine sites are converted to plantations (Repenning and Labisky 1985). Under primeval conditions, the arthropod biomass consumed by the red-cockaded woodpecker must have been very large. Many species of woodpeckers, from a range of habitats, are voracious feeders on dendrophagous insects (Barbosa and Wagner 1989). Bruns (1960) found that providing artificial nest boxes for birds resulted in a 100-fold reduction in the number of pine loopers per tree. It seems likely that the essential absence of the red-cockaded woodpecker from most longleaf pine habitats has significantly affected the arthropod fauna. It is unlikely that the precise effects can ever be assessed.

### Effects of introduced species

A number of exotic animal species in the southeastern United States undoubtedly interact with native arthropods. We mention three introduced species that may have significantly affected arthropods of longleaf pine habitats.

The common long-nosed armadillo, *Dasypus novemcinctus*, has spread from Mexico and release sites in Florida through much of the southeastern United States. In recent years, it has crossed the Fall Line in Alabama and has invaded several upland provinces. The armadillo now exists in large numbers in longleaf pine habitats from Texas to Florida and Georgia. Although it is more common in moister sites, it also occurs in sandhills and dry longleaf pine savannas.

All reports of the food habits of this species in the U.S. indicate that it is primarily insectivorous, with beetles and ants major components of the diet (Fitch et al. 1952, Breece and Dusi 1985, Wirtz et al. 1985). Individuals feed by digging and probing, usually in sites where litter is abundant. As abundant as this species has become, it is almost certain that it has affected the arthropod fauna. Ground-dwelling beetles, especially those associated with litter, such as a number of carabids, are the types most likely to have been affected. In sites with thin litter, ants and termites are probably the most common prey, as they are in tropical areas of the species range (Redford 1985). Because we have

little quantitative data on the fauna before the arrival of the armadillo, it may not be possible to assess its effects in most of the Southeast. However, data can still be gathered in longleaf pine habitats in portions of Georgia and the Carolinas which the animal may not yet have invaded. At sites in the Georgia Fall Line sandhills, *Geolycosa patellonigra* may be present in populations as dense as 8/m<sup>2</sup>. More southerly sites, already invaded by the armadillo, seldom harbor such dense populations.

The honey bee, *Apis mellifera*, was introduced to North America from Europe early in the history of European settlement of the continent. It has probably been a part of the fauna of the southeastern United States for at least two hundred years. Because of its abundance in many areas, the honeybee is a major gatherer of pollen and nectar from the flowers of many angiosperm species. Its effectiveness in pollinating wild plants is unknown, however, it is probably a significant competitor for many small and medium-sized native bees. It is possible that the honey bee drove some native species to extinction before they were discovered by early entomologists. Lack of effective pollination by the honeybee may have resulted in changes in the relative abundance of certain plant species. Native bee species may have been reduced to such low abundance that some of the plants that depend on them for pollination may have decreased levels of sexual reproduction. Any of these changes could have had ramifications throughout the longleaf pine system and conceivably have affected the abundance of a number of native arthropod species.

The red imported fire ant, *Solenopsis invicta*, and the black imported fire ant, *S. richteri*, were introduced into the southeastern United States in the first half of the century. Both species may be found in longleaf pine habitats but the red imported fire ant is more common and widespread. In xeric sites where little disturbance has occurred, few fire ants are present. However, disturbance of the soil seems to facilitate fire ant colonization (Tschinkel 1988), although they never reach the densities found in moister sites. Fire ants readily prey on other insects and may affect the abundance of some species (Harris and Burns 1972). Additionally, competition has apparently affected the abundance of some native ant species (Porter et al. 1988, Tschinkel 1988). *Solenopsis invicta* is likely to reduce biological diversity in many habitats in the southeastern United States. The extent to which imported fire ants have impacted the arthropod fauna of xeric longleaf pine sites is unknown.

## CONCLUSIONS

Knowledge of the arthropod fauna and its functioning in xeric longleaf pine habitats is inadequate, although this group of organisms is clearly of major significance in the system. If we are to preserve, manage or rehabilitate these habitats, more detailed information on the arthropod fauna must be obtained. Some information on the presence, life history, and effects of arthropods can easily be obtained during many ongoing studies, often with minimal effort. Most research plans should include some consideration of the possible role of arthropods. Investigators should keep in mind that this group of organisms is probably significant in every phenomenon in which they are interested.

This work is increasingly handicapped by the decrease in skilled taxonomists needed to identify the great diversity of arthropods. This worldwide problem will hamper the development of biological knowledge if it is not immediately redressed.

Research stations, field laboratories, and government land management agencies can play an important role in stimulating research involving arthropods. However, most of these groups and organizations have ignored or are unaware of opportunities in arthropod research. Of over a dozen formally organized research areas, stations, or laboratories that exist in the range of longleaf pine, only

one had a professional entomologist on staff in 1990. Few have any type of ongoing program designed to monitor or survey the arthropod fauna on their sites. The U.S. Forest Service has hired botanists, but employs no entomologists except those hired to study the effects of insects on commercially important trees.

Not only will studies of the arthropod fauna produce worthwhile scientific information, but knowledge and awareness of the fauna will enhance our appreciation of a habitat that we all already prize as unique, fascinating, and certainly worth preserving.

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## APPENDIX I

### LIST OF ANT SPECIES KNOWN TO INHABIT XERIC LONGLEAF PINE HABITATS IN THE SOUTHEASTERN UNITED STATES

SPECIES	COMMENTS
<i>Amblyopone pallipes</i>	rare, usually associated with dead wood, never forages above ground
<i>Aphaenogaster ashmeadi</i>	usually in rather overgrown sites, diurnal forager
<i>Aphaenogaster floridana</i>	open sites, often active at night, nest often with conspicuous turret
<i>Aphaenogaster treatae</i>	open sites
<i>Brachymyrmex depilis</i>	bases of pines, seldom forages in open
<i>Brachymyrmex obscurior</i>	open sites, often associated with human disturbance, often forages in open
<i>Camponotus nearcticus</i>	nests in branches of large pines
<i>Camponotus psocius</i>	nests in soil in open areas
<i>Conomyrma bureni</i>	common, in open sand and bases of tussocks
<i>Conomyrma elegans</i>	southern Lake Wales Ridge only, sandhills
<i>Conomyrma grandula</i>	exact habitat unknown
<i>Crematogaster ashmeadi</i>	arboreal, common in dead twigs and branches of oaks, less common in pine
<i>Crematogaster cerasi</i>	common, in leaf litter and tussocks
<i>Crematogaster minutissima</i>	occasional, in open areas
<i>Crematogaster</i> n. sp.	arboreal in large pines, nests under bark
<i>Forelius pruinosus</i>	common in open areas and bases of tussocks
<i>Formica archboldi</i>	moderately common, west-central Florida, usually in sites with rather dense ground cover

## APPENDIX I (CONT.)

<i>Formica pallidefulva</i>	commonest sandhill <i>Formica</i> , in sparsely vegetated sites
<i>Hypoponera opacior</i>	common in leaf litter and tussocks, never forages above ground
<i>Leptothorax pergandei</i>	common, in leaf litter, nests in hollow buried twigs
<i>Leptothorax texanus</i>	common, in open sand with lichens
<i>Monomorium viride</i>	common, in open areas
<i>Neivamyrmex texanus</i>	apparently rare
<i>Odontomachus brunneus</i>	common, north-central peninsular Florida, in both open and shaded sites
<i>Odontomachus clarus</i>	common, restricted to southern Lake Wales Ridge of peninsular Florida
<i>Paratrechina arenivaga</i>	common in open sites
<i>Pheidole bicarinata</i>	open sandy areas, commoner northward
<i>Pheidole floridana</i>	usually at the bases of pines, in layers of bark at root collar
<i>Pheidole morrisi</i>	most abundant <i>Pheidole</i> of sandhills, in open sand
<i>Pogonomyrmex badius</i>	common, requires open sand
<i>Polyergus lucidus</i>	enslaves <i>Formica archboldi</i> , rare
<i>Smithistruma dietrichi</i>	rare, in litter at bases of stumps
<i>Smithistruma ornata</i>	common, in pockets of litter, does not forage on surface
<i>Smithistruma talpa</i>	common, in pockets of litter, does not forage on surface
<i>Solenopsis carolinensis</i>	in soil, tussocks, litter, does not forage on surface
<i>Solenopsis geminata</i>	common, but becoming rarer as a result of invasion by <i>S. invicta</i>
<i>Solenopsis invicta</i>	common, especially in disturbed sites
<i>Solenopsis pergandei</i>	common, in open sand
<i>Trachymyrmex septentrionalis</i>	common, in both open and moderately shaded sites, makes conspicuous semi-circular mound of sand pellets

## APPENDIX II

### ARTHROPOD SPECIES FOUND AS OBLIGATE ASSOCIATES AND FREQUENT INQUILINES IN BURROWS OF THE GOPHER TORTOISE, *Gopherus polyphemus*

(compiled from Young and Goff 1939, Woodruff 1982a, Millstrey 1986, Lago 1991, and others)

SCIENTIFIC NAME (CLASSIFICATION)	COMMENTS
<i>Chelanops affinis</i> (Pseudoscorpiones: Chernetidae)	predator, obligate associate
<i>Crosbyella</i> sp. (Opiliones: Phalangodidae)	obligate associate
<i>Amblyomma tuberculatum</i> (Acari: Ixodidae)	adults normally restricted to the gopher tortoise, largest New World tick
<i>Ceuthophilus latibuli</i> (Orthoptera: Gryllacrididae)	often numerous, occurs in other habitats
<i>Eutrichota gopheri</i> (Diptera: Anthomyiidae)	larvae feed on tortoise dung
<i>Machimus</i> sp. (Diptera: Asilidae)	preys on <i>Eutrichota</i> , obligate
<i>Spelobia</i> sp. (Diptera: Sphaeroceridae)	larvae feed on tortoise dung
<i>Epizeuxis gopheri</i> (Lepidoptera: Noctuidae)	larvae prefer fresh tortoise dung
<i>Acrolophus pholeter</i> (Lepidoptera: Tineidae)	larvae feed on dung and decaying plant debris
<i>Ptomophagus texanus</i> (Coleoptera: Leiodidae)	frequent, but not obligate
<i>Acrostilscus hospes</i> (Coleoptera: Staphylinidae)	very rare, may be obligate
<i>Philonthus gopheri</i> (Coleoptera: Staphylinidae)	pale color indicates subterranean habit, obligate associate
<i>Trichopteryx</i> sp. (Coleoptera: Ptiliidae)	possibly an obligate associate
<i>Chelyoxenus xerobatis</i> other(Coleoptera: Histeridae)	relict genus, larvae may feed on burrow inhabitants, obligate associate

## APPENDIX II (CONT.)

*Copris gopheri*  
(Coleoptera: Scarabaeidae)

sometimes abundant, larvae develop in  
balls of dung, obligate associate

*Onthophagus polyphemi*  
(Coleoptera: Scarabaeidae)

obligate associate

*Aphodius troglodytes*  
(Coleoptera: Scarabaeidae)

present in almost every burrow, pale with  
reduced eyes, obligate associate

### APPENDIX III

#### ARTHROPOD SPECIES FOUND AS OBLIGATE ASSOCIATES AND FREQUENT INQUILINES IN BURROWS OF THE SOUTHEASTERN POCKET GOPHER, *Geomys pinetus*

(compiled from Hubbell and Goff 1939, Woodruff 1973, 1982b, and others )

SCIENTIFIC NAME (CLASSIFICATION)	COMMENTS
<i>Eulithobius hypogeus</i> (Chilopoda: Lithobiidae)	obligate, preys on other associates
<i>Pholobius goffi</i> (Chilopoda: Lithobiidae)	obligate, preys on other associates
<i>Sosilaus spiniger</i> (Araneae: Lycosidae)	obligate, preys on other associates
<i>Nicoletia</i> sp. (Thysanura: Lepismatidae)	obligate, blind and nearly white in color
<i>Pseudosinella violenta</i> (Collembola: Entomobryidae)	large for a springtail, sometimes abundant
<i>Ceuthophilus latibuli</i> (Orthoptera: Gryllacrididae)	also found in gopher tortoise burrows
<i>Typhloceuthophilus floridanus</i> (Orthoptera: Gryllacrididae)	obligate, completely blind
<i>Spilodiscus floridanus</i> (Coleoptera: Histeridae)	obligate, associated with <i>Geomys</i> dung
<i>Atholus minutus</i> (Coleoptera: Histeridae)	presumed obligate, associated with dung
<i>Geomysaprinus goffi</i> (Coleoptera: Histeridae)	obligate, associated with dung
<i>Geomysaprinus tibialis</i> (Coleoptera: Histeridae)	obligate, associated with dung
<i>Aphodius aegrotus</i> (Coleoptera: Scarabaeidae)	obligate, feeds on dung, common
<i>Aphodius haldemani</i> (Coleoptera: Scarabaeidae)	also occurs with western <i>Geomys</i>
<i>Aphodius laevigatus</i> (Coleoptera: Scarabaeidae)	obligate, feeds on dung, common
<i>Amydria</i> sp. (Lepidoptera: Tineidae)	obligate, feeds on dung or perhaps hair
<i>Pegomyia</i> sp. (Diptera: Anthomyiidae)	obligate, feeds on dung or perhaps plant material

## APPENDIX IV

### LIST OF ARTHROPOD SPECIES KNOWN TO ATTACK UNWEAKENED LONGLEAF PINE (*Pinus palustris*) TREES WITHIN THE NATIVE RANGE OF THE SPECIES

COMMON NAME	SCIENTIFIC NAME (CLASSIFICATION)	COMMENTS
red mite (Acari: Tetranychidae)	<i>Oligonychus cunliffei</i>	tiny, attacks foliage, tiny, attacks foliage, strands of webbing may be visible
stink bug	<i>Brochymena carolinensis</i> (Heteroptera: Pentatomidae)	feeds through bark
shieldbacked pine seed bug	<i>Tetyra bipunctata</i> (Heteroptera: Pentatomidae)	feeds through cones, penetrates seeds
leaf-footed pine seed bug	<i>Leptoglossus corculus</i> (Heteroptera: Coreidae)	attacks developing ovules and seeds
southern pine aphid (Homoptera: Aphididae)	<i>Cinara atlantica</i>	dense colonies on twigs, may be protected by by ants, sooty mold on honeydew may be obvious
mealybug	<i>Oracella acuta</i> (Homoptera: Pseudococcidae)	in whitish resinous cell attached to twigs near needle bases
wooly pine scale	<i>Pseudophillipia quaintancii</i> (Homoptera: Coccidae)	covered with white fleecy secretion
pine tortoise scale	<i>Toumeyella parvicornis</i> (Homoptera: Coccidae)	foliage, first found during this study
Virginia pine scale	<i>Toumeyella virginiana</i> (Homoptera: Coccidae)	often beneath bark
southern pine scale	<i>Chionaspis heterophyllae</i> (Homoptera: Diaspididae)	dense populations may whiten foliage
black pineleaf scale	<i>Nuculaspis californica</i> (Homoptera: Diaspididae)	dark oval scale covering
Louisiana longleaf needleminer	<i>Holocera lepidophaga</i> (Lepidoptera: Blastobasidae)	attacks male cones, young cones, vegetative buds
pine needleminer	<i>Coleotechnites chillcotti</i> (Lepidoptera: Gelechiidae)	young larvae mine needles, older larvae tie leaves together, local in mid-Gulf region, one of the two monophagous species on longleaf pine
	<i>Exoteleia pinifoliella</i> (Lepidoptera: Gelechiidae)	mines needles longleaf pine not preferred host
	<i>Battaristis vittella</i> (Lepidoptera: Gelechiidae)	attacks cones
southern pine coneworm	<i>Dioryctria amatella</i> (Lepidoptera: Pyralidae)	may cause heavy cone losses
blister coneworm	<i>Dioryctria clarioralis</i> (Lepidoptera: Pyralidae)	buds, conelets, cones
webbing coneworm	<i>Dioryctria disclusa</i> (Lepidoptera: Pyralidae)	attack sporadic, frass in webbing over entrance hole to hollowed cone

## APPENDIX IV (CONT.)

south coastal coneworm	<i>Dioryctria ebeli</i> (Lepidoptera: Pyralidae)	attacks mainly diseased or damaged cones
loblolly pine coneworm	<i>Dioryctria merkei</i> (Lepidoptera: Pyralidae)	immature cones, cones, shoots
pine webworm	<i>Tetralopha robustella</i> (Lepidoptera: Pyralidae) mine needles	attacks foliage, globular masses of frass tied together with webbing, young larvae
slash pine seedworm	<i>Cydia anaranjada</i> (Lepidoptera: Tortricidae)	only occasionally attacks longleaf pine
longleaf pine seedworm	<i>Cydia ingens</i> (Lepidoptera: Tortricidae)	one of two herbivorous arthropods for which longleaf pine is the preferred host, larva devours internal portion of seed
European pine shoot moth	<i>Rhyacionia buoliana</i> (Lepidoptera: Tortricidae)	introduced from Europe, not common in most areas of southeastern U.S.
subtropical pine tip moth	<i>Rhyacionia subtropica</i> (Lepidoptera: Tortricidae)	slash pine preferred host, attacks longleaf pine only within range of slash pine
turpentine wood borer	<i>Buprestis apricans</i> (Coleoptera: Buprestidae)	larvae bore in wood riddling may cause proneness to wind breakage
metallic wood borer	<i>Buprestis lineata</i> (Coleoptera: Buprestidae)	larvae bore in wood
metallic wood borer	<i>Chrysobothris dentipes</i> (Coleoptera: Buprestidae)	mainly attacks stressed plants
metallic wood borer	<i>Chrysobothris floricola</i> (Coleoptera: Buprestidae)	mainly attacks stressed plants
deodar weevil	<i>Pissodes nemorensis</i> (Coleoptera: Curculionidae)	smaller trees, attacks bud on young shoots, larvae under bark

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