

## Review

# Arthropods and Fire Within the Biologically Diverse Longleaf Pine Ecosystem

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## Abstract

The longleaf pine *Pinus palustris* Miller (Pinales: Pinaceae) ecosystem once covered as many as 37 million hectares across the southeastern United States. Through fire suppression, development, and conversion to other plantation pines, this coverage has dwindled to fewer than 2 million hectares. A recent focus on the restoration of this ecosystem has revealed its complex and biologically diverse nature. Arthropods of the longleaf pine ecosystem are incredibly numerous and diverse—functionally and taxonomically. To provide clarity on what is known about the species and their functional roles in longleaf pine forests, we thoroughly searched the literature and found nearly 500 references. In the end, we tabulated 51 orders 477 families, 1,949 genera, and 3,032 arthropod species as having been stated in the scientific literature to occur in longleaf pine ecosystems. The body of research we drew from is rich and varied but far from comprehensive. Most work deals with land management objective associated taxa such as pests of pine, pests of—and food for—wildlife (red-cockaded woodpecker, northern bobwhite quail, gopher tortoise, pocket gopher, etc.), and pollinators of the diverse plant understory associated with longleaf pine. We explored the complex role frequent fire (critical in longleaf pine management) plays in determining the arthropod community in longleaf pine, including its importance to rare and threatened species. We examined known patterns of abundance and occurrence of key functional groups of longleaf pine-associated arthropods. Finally, we identified some critical gaps in knowledge and provide suggestions for future research into this incredibly diverse ecosystem.

**Key words:** insect, biodiversity, invertebrate, conservation

The arthropods of the longleaf pine *Pinus palustris* Miller ecosystem (hereafter LLPE) are an immense, diverse, and understudied group. An initial review on the subject (Folkerts et al. 1993) gave a sense of the many arthropods found in this incredibly diverse woodland ecosystem. In the decades since, we have learned more about the diversity and functional roles of many organisms, and the restoration of this once dominant ecosystem has become a major conservation priority (Kirkman and Jack 2017). Our purpose here is to gather more recent literature and synthesize the state of knowledge, identifying and prioritizing important gaps therein. To complement and inform this synthesis, we tabulated all the species we could find in the literature and our collecting efforts (Supp Tables 1 and 2 [online only]). While broad generalizations are difficult to make, and there may be exceptions to conclusions we draw, we have endeavored to cover the extensively diverse taxa within the heterogenous habitats found in the LLPE. Unless otherwise explicitly stated, we consider a species

to be ‘characteristic’ of longleaf pine if it has been documented in a study whose methods state that the study site consisted of longleaf pine habitat. Arthropods play numerous and diverse ecological roles; it is impossible to analyze these roles exhaustively and fully in a single review article. While we have focused here on terrestrial arthropods in longleaf pine (hereafter, LLP) woodlands, it is worth noting that LLPEs may also contain marshes, wetlands, streams, and rivers. For example, the LLPE at the Jones Center at Ichauway—an extremely diverse longleaf pine dominated property and research center—includes ephemeral streams, isolated wetlands, and swampy areas (Smith et al. 2017). In arthropod work there, Smith and Golladay (2014) found curculionid weevils in moist environments and wetland vegetation. A sampling of 24 isolated wetlands (marshes, savannas, or forested swamps) found 27 species within 17 genera. Both isolated wetlands and hardwood depressions that exist within the LLPE support arthropods (Golladay et al. 1997,

1999; Battle et al. 2001; Battle and Golladay 2002). Adults of other aquatic species forage in the terrestrial LLPE [e.g., the LLPE endemic *Cordulegaster sayi* Selys (Odonata: Cordulegasteridae) (Stevenson et al. 2009)]. Additional information on aquatic species is found in Supp Table 1 (online only).

### Longleaf Pine Past Extent, Threats, and Restoration

Longleaf pine became dominant in the North American Coastal Plain only ~4,000–8,000 yr before the present, after glaciers retreated (Van Lear et al. 2005, Oswalt et al. 2012). At their peak, longleaf pine communities covered as many as 37 million hectares (Frost 2006) across much of the southeastern United States, representing up to 90% of the landscape in some areas (Oswalt et al. 2012). One million hectares, about 2.2% of its original range, remained by 2005 (Oswalt et al. 2012). This reduction was largely due to fire exclusion, land development, and the conversion to other pine plantation species, such as loblolly pine *P. taeda* L., or slash pine *P. elliotii* Engelm (Kirkman et al. 2017). Recent catastrophic storm damage has additionally reduced the extent of longleaf; as much as 28% of the total amount of the LLPE was affected by Hurricane Michael in Florida, USA alone (Zampieri et al. 2020), even though longleaf pine is generally more resilient than other pines to storm damage, insects, and disease (Johnsen et al. 2009, Clark et al. 2018). Unsurprisingly, old-growth longleaf pine has been even further devastated, with estimates of only 5,095 hectares remaining, which represents a mere 0.00014% of presettlement longleaf extent (Varner and Kush 2004).

Considered one of the ‘21 most-endangered ecosystems in the United States’, the LLPE contained 27 federally listed species and 99 candidate species in 1995 (Noss and Peters 1995). More recently, 30 species of organisms within the LLPE are federally listed as endangered with over 50 additional species listed as at-risk (McIntyre et al. 2018). The LLPE is home to a significantly rich flora and fauna within the North American Coastal Plain, a global biodiversity hotspot (Noss et al. 2015).

Since the late 1990s, there has been a concerted effort to restore the LLPE, in part due to the success of programs to protect and restore the red-cockaded woodpecker *Leuconotopicus borealis* (Viellot)—an endangered longleaf pine specialist (McIntyre et al. 2017), now proposed to being down-listed to threatened status (U.S. Fish and Wildlife Service 2020). In 2009, the America’s Longleaf Restoration Initiative set a goal of furthering the extent of LLP to at least 3.24 million hectares by 2025 (McIntyre et al. 2018). The most recent estimate of longleaf pine habitat is ~1.85 million hectares (USDA Forest Service FIA 2021).

Frequent fire is essential to the sustainability, resilience, and integrity of the LLPE, which means that prescribed fire is a critical management tool necessary for maintaining the LLPE (Mitchell et al. 2006; Fig. 1). Frequent fire prevents hardwood dominance, allows for regeneration of longleaf pine and its associated understory, and preserves an open canopy (Kirkman et al. 2017). Historically, ignition sources have been lightning (Outcalt 2008), intentional fires set by indigenous populations for hunting purposes (Anderson and Barbour 2003, Oswalt et al. 2012), fires set by early European colonizers to improve cattle foraging (Oswalt et al. 2012), and now organized programs of regular controlled burns (Kirkman and Jack 2017). In addition to *P. palustris*, the ecosystem may contain other pine species, hickory *Carya* spp. (Gilliam and Platt 1999), and pyrophytic (adapted to tolerate fire) oaks *Quercus* spp., which are

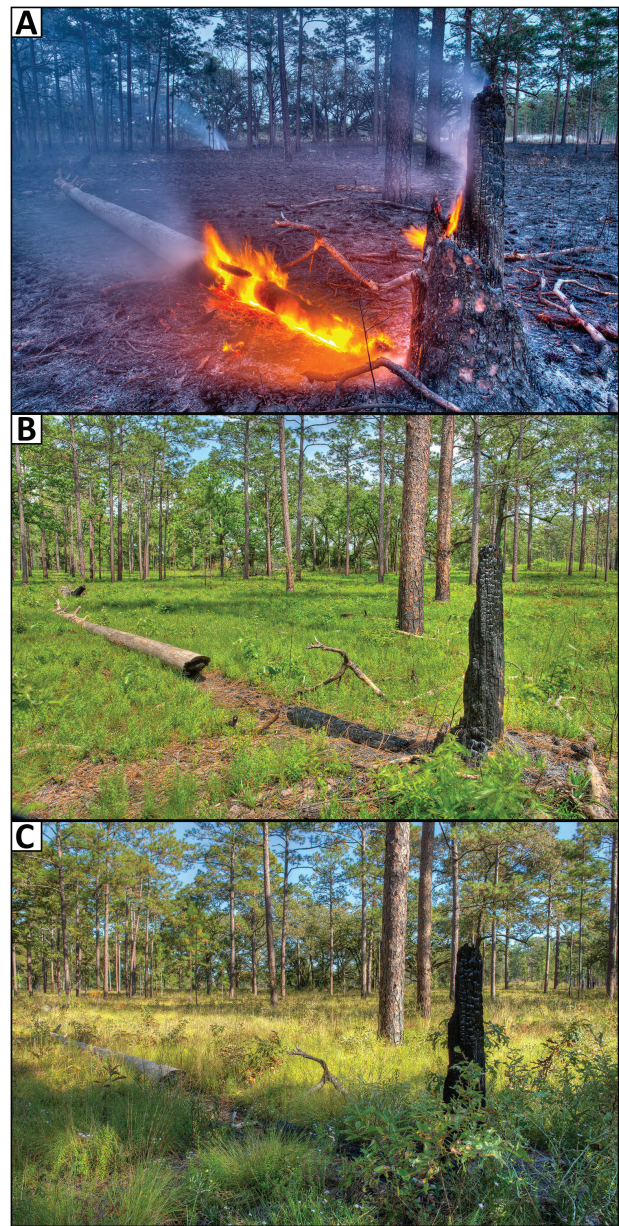


Fig. 1. Natural longleaf pine stand during burn (A), 2 mo post-burn (B), and 6 mo post-burn (C). The diverse herbaceous groundcover of this system requires frequent fire to maintain an open canopy and allow natural regeneration. Photography courtesy of Richard T. Bryant.

often a critical component of the ecosystem (Hiers et al. 2014), and other hardwoods in pockets of fire exclusion.

### Longleaf Pine Flora and Fauna

The LLPE boasts one of the most species-rich plant communities in temperate regions (Walker 1993, Kirkman et al. 2004, Platt et al. 2006, Kirkman and Giencke 2017). It contains nearly 200 rare vascular plants, of which 96 are local endemics (Walker 1993). This ecosystem includes areas with groundcover diversity as high as over 40 species per m<sup>2</sup> and up to 140 species per 1,000 m<sup>2</sup> (Peet and Allard 1993). Notable families include Asteraceae, Fabaceae, and Poaceae, especially wiregrass *Aristida stricta* Michx., characteristic of undisturbed sites in much of longleaf’s eastern range. For further

discussion of ground cover diversity in the LLPE, see Kirkman and Giенcke (2017). Soil, topography, canopy openness, and disturbance (e.g., fire) influence plant diversity in the LLPE (Kirkman et al. 2004; Platt et al. 2006; Carr et al. 2009, 2010).

Relative to arthropods, the immensely diverse vertebrates of the LLPE are well-documented by reviews in the literature (Engstrom 1993; Stout and Marion 1993; Guyer and Bailey 1993; Dodd 1995; Means 2006; Smith et al. 2006, 2017). Throughout its entire range, the LLPE contains about nine species of salamanders, 26 species of frogs, 29 species of snakes, 14 species of lizards, 1 species of amphibiaenian, 10 species of turtles, 88 species of birds, 40 species of mammals that are either characteristic of or endemic to the LLPE, and an additional 71 species that may have once been characteristic but are no longer (Means 2006). Of particular note, a new salamander species—the reticulated siren *Siren reticulata* Graham, Kline, Steen, & Kelehear—was discovered as recently as 2018 within the broader LLPE (Graham et al. 2018). Management considerations for vertebrates include the value of upland habitat near seasonal wetlands, structures such as dead trees, stumps, tree bases, and prescribed fire (Means 2006, Smith et al. 2017). These management considerations likely overlap with many arthropod habitat requirements.

### Longleaf Pine Arthropods Overview

The minimum number of arthropod species in xeric longleaf pine habitats is conservatively estimated at 4,000–5,000 species, though even this may be an underestimate (Folkerts et al. 1993). A single 5-yr study of ground-dwelling arthropods in the LLPE produced over 163,000 arthropods from 31 orders, 265 families, and 932 genera (Hanula and Wade 2003). A 2-yr study of four longleaf preserves focused only on moths, butterflies, and grasshoppers collected 28 families and 512 species (Hall and Schweitzer 1993). The highest within-habitat species richness (72 species) ever recorded for North American ants was found in the LLPE in northern Florida (Lubertazzi and Tschinkel 2003). In another study, 53 ant species were collected in the LLPE of the Welaka Reserve, Florida (Van Pelt 1956, 1958). As displayed in Supp Table 2 (online only), we thoroughly searched the literature for mentions of arthropod taxa in the LLPE (including embedded wetlands) and categorized them by taxonomic groups. Wherever possible and appropriate, we updated names to the most current taxonomy.

From a subset of this literature, we were able to document terrestrial arthropod species in the LLPE. In 7,395 rows of taxa mentioned in the literature, we counted 51 orders, 477 families, 1,949 genera, and 3,032 species (Supp Table 1 [online only]). The total number of arthropod species in the LLPE is undoubtedly higher. There are certain species we missed in our search, as well as instances not reported in the literature, not determined to species resolution, not yet described, and not even collected by humans. Examples of species described from the LLPE in the past 10 yr include *Scarites stenops* Bousquet & Skelley (Coleoptera: Carabidae), *Dineutus shorti* Gustafson and Sites (Coleoptera: Gyrinidae), *Onthophilus burkei* Kovarik & Skelley (Coleoptera: Histeridae), and seven species of *Melanoplus* (Orthoptera: Acrididae) (Supp Table 2 [online only]). We present an additional 41 species previously undocumented in the LLPE (Table 1 and Fig. 2). Voucher specimens were deposited in the UGA Collection of Arthropods of the Georgia Museum of Natural History.

Many of the most diverse orders are generally well represented in our tabulation. Hymenoptera, Lepidoptera, Coleoptera, Diptera, Araneae, Orthoptera, and Hemiptera all account for over a hundred

**Table 1.** Arthropod species undocumented in the longleaf pine ecosystem prior to recent collecting at the Jones Center at Ichauway

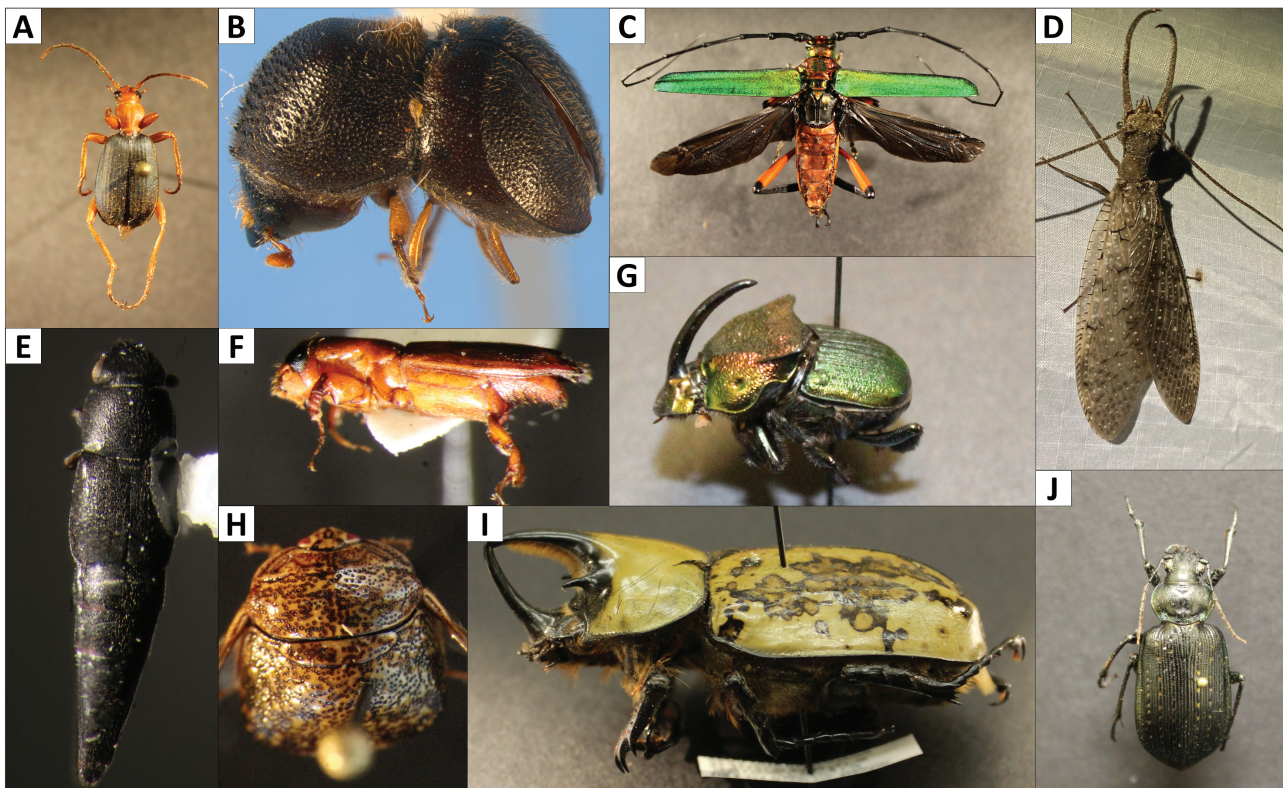
Order	Family	Species
Araneae	Araneidae	<i>Gasteracantha cancriformis</i> Linnaeus
Araneae	Araneidae	<i>Trichonephila clavipes</i> (Linnaeus)
Araneae	Tetragnathidae	<i>Leucage venusta</i> (Walckenaer)
Araneae	Thomisidae	<i>Bassaniana</i> sp.
Coleoptera	Anthicidae	<i>Notoxus murinipennis</i> LeConte
Coleoptera	Carabidae	<i>Ardistomis schaumii</i> LeConte
Coleoptera	Carabidae	<i>Brachinus</i> sp.
Coleoptera	Carabidae	<i>Calosoma sayi</i> Dejean
Coleoptera	Carabidae	<i>Cratacanthus dubius</i> (Palisot de Beauvois)
Coleoptera	Carabidae	<i>Pseudomorpha exrucians</i> Kirby
Coleoptera	Carabidae	<i>Scarites subterraneus</i> Fabricius
Coleoptera	Carabidae	<i>Tetracha carolina</i> (Linnaeus)
Coleoptera	Carabidae	<i>Tetragonoderus intersectus</i> (Germar)
Coleoptera	Cerambycidae	<i>Batyle ignicollis</i> (Say)
Coleoptera	Cerambycidae	<i>Leptostylus transversus</i> (Gyllenhal)
Coleoptera	Cerambycidae	<i>Nyssodrysin haldemani</i> (LeConte)
Coleoptera	Cerambycidae	<i>Plinthocoelium suaveolens</i> (Linnaeus)
Coleoptera	Cerambycidae	<i>Scaphinus muticus</i> (Fabricius)
Coleoptera	Cleridae	<i>Cymatodera wolcottii</i> Barr
Coleoptera	Curculionidae	<i>Cnesinus strigicollis</i> LeConte
Coleoptera	Curculionidae	<i>Cnestus mutilatus</i> (Blandford) <sup>a</sup>
Coleoptera	Curculionidae	<i>Dryoxylon onoharaense</i> (Murayama) <sup>a</sup>
Coleoptera	Curculionidae	<i>Euplatypus compositus</i> (Say)
Coleoptera	Curculionidae	<i>Hylocurus rudis</i> (LeConte)
Coleoptera	Curculionidae	<i>Monarthrum fasciatum</i> (Say)
Coleoptera	Curculionidae	<i>Myoplatypus flavicornis</i> Fabricius
Coleoptera	Nitidulidae	<i>Carpophilus mutilatus</i> Erichson
Coleoptera	Nitidulidae	<i>Conotelus obscurus</i> Erichson
Coleoptera	Nitidulidae	<i>Lobiopa insularis</i> (Laporte)
Coleoptera	Scarabaeidae	<i>Deltochium gibbosum</i> (Fabricius)
Coleoptera	Scarabaeidae	<i>Dynastes tityus</i> Linnaeus
Coleoptera	Scarabaeidae	<i>Phanaeus vindex</i> (Hentz)
Coleoptera	Scarabaeidae	<i>Strategus aloeus</i> (Linnaeus)
Coleoptera	Scarabaeidae	<i>Strategus antaeus</i> (Drury)
Coleoptera	Silphidae	<i>Nicrophorus carolina</i> (Linnaeus)
Coleoptera	Staphylinidae	<i>Creophilus maxillosus</i> (Linnaeus)
Diptera	Bibionidae	<i>Plecia nearctica</i> Hardy
Diptera	Syrphidae	<i>Microdon</i> sp.
Hemiptera	Coreidae	<i>Acanthocephala declivis</i> (Say)
Hemiptera	Plataspidae	<i>Megacopta cribraria</i> (Fabricius) <sup>a</sup>
Neuroptera	Corydalidae	<i>Corydalis cornutus</i> (Linnaeus)

<sup>a</sup>Exotic to North America.

species each and (except for Orthoptera) dozens of families (Table 2).

Families with more than 50 species documented in the LLPE include ants (Hymenoptera: Formicidae,  $n = 253$ ), erebid moths (Lepidoptera: Erebidae,  $n = 163$ ), owl moths (Lepidoptera: Noctuidae,  $n = 163$ ), weevils (Coleoptera: Curculionidae,  $n = 122$ ), grasshoppers (Orthoptera: Acrididae,  $n = 116$ ), geometer moths (Lepidoptera: Geometridae,  $n = 109$ ), sweat bees (Hymenoptera: Halictidae,  $n = 80$ ), apid bees (Hymenoptera: Apidae,  $n = 76$ ), mason bees (Hymenoptera: Megachilidae,  $n = 67$ ), scarab beetles (Coleoptera: Scarabaeidae,  $n = 61$ ), and ground beetles (Coleoptera: Carabidae,  $n = 59$ ; Supp Table 3 [online only]).

In contrast, a few examples of notable families with only a single species represented include cicadas (Hemiptera: Cicadidae), treehoppers (Hemiptera: Membracidae), green lacewings (Neuroptera: Chrysidae), carpet beetles (Coleoptera: Dermestidae), false click beetles (Coleoptera: Eucnemidae), hide beetles (Coleoptera: Trogidae), bee



**Fig. 2.** Arthropod species undocumented in the longleaf pine ecosystem before recent collecting at the Jones Center at Ichauway. For full list, see [Table 1](#). (A) *Brachinus* sp. (B) *Cnestus mutilatus*\*, (C) *Plinthocoelium suaveolens*, (D) *Corydalus cornutus*, (E) *Conotelus obscurus*, (F) *Euplatypus compositus*, (G) *Phanaeus vindex*, (H) *Megacopta cribraria*\*, (I) *Dynastes tityus*, (J) *Calosoma sayi*. \*Exotic to North America.

flies (Diptera: Bombyliidae), leaf miner flies (Diptera: Agromyzidae), dance flies (Diptera: Empididae), mydas flies (Diptera: Mydidae), picture-winged flies (Diptera: Ulidiidae), and marsh flies (Diptera: Sciomyzidae). In total, 255 families are only represented by a single species or were only determined to family or genus. Further investigation and taxonomic resolution would undoubtedly reveal a multitude of additional species. All orders of insects, and most orders of arthropods, whose ranges co-occur with the LLP have been documented in the LLPE. Even cryptic taxa such as twisted wing parasites (Strepsiptera), earwigflies (Mecoptera: Meropeidae), and web-spinners (Embiidina) have been collected in the LLPE (Folkerts et al. 1993, Hooper 1996, Hanula and Wade 2003, Dunford et al. 2007). Galley and Flowers (1998) rediscovered a springtail species and a grasshopper species in the LLPE, both of which had been previously searched for without success.

Pests of mature trees harvested for timber [e.g., pine engraver beetles *Ips* spp., pine sawyer beetles *Monochamus* spp., black turpentine beetle *Dendroctonus terebrans* (Olivier), and southern pine beetle *Dendroctonus frontalis* Zimmerman] are relatively well represented in the LLPE literature. This is primarily due to the prevalence of these pests in pine systems and their economic and ecological impacts. Other LLPE arthropod surveys have focused on particular taxa: lepidopterans (Hall and Schweitzer 1993, Kerstyn and Stiling 1999, Landau and Prowell 1999, Prowell 2001), bees (see Herbaceous Layer), ants (see Forest Floor section), arachnids (Corey and Taylor 1987, Corey and Stout 1990, Corey et al. 1998), myriapods (Scheller 1988, Corey and Stout 1992), and orthopterans (Rehn and Hebard 1907; Friauf 1953; Hall and Schweitzer 1993; Kerstyn and Stiling 1999; Hill and MacGown 2008; Hill 2009, 2015).

Just as certain mammal species have been extirpated and replaced by recently invading mammals (Engstrom 1993), arthropod species have likely been lost and replaced. Exotic invasive arthropods have certainly infiltrated into the LLPE, e.g., the red imported fire ant *Solenopsis invicta* Buren (hereafter, ‘fire ant’) and redbay ambrosia beetle *Xyleborus glabratus* Eichhoff (Brar et al. 2012). We report three species exotic to North America previously undocumented in the LLPE: two ambrosia beetles—*Cnestus mutilatus* (Blandford) and *Dryoxylon onoharaense* (Murayama)—and the kudzu bug *Megacopta cribraria* (Hemiptera: Plataspidae) (Table 1 and Fig. 2). Due to their smaller size, more cryptic behavior, and lack of study, the number of extirpated or extinct arthropod species seems difficult (and likely impossible) to determine. We currently know of no fossil arthropods from the LLPE, which may not be surprising due to the LLPE’s relatively young age and the infrequency of arthropod fossils in general.

### Vulnerability of Arthropod Populations

Numerous researchers have documented the loss of arthropod biomass and diversity in various locations around the world (Potts et al. 2010, Sánchez-Bayo and Wyckhuys 2019, Eggleton 2020, Wagner 2020). More specifically, declines have been attributed to land-use intensification (Sorg et al. 2013, Hallmann et al. 2017, Seibold et al. 2019), agricultural intensification (Raven and Wagner 2020), insecticide use (Hallmann et al. 2014, Siviter and Muth 2020), climate change (Lister and Garcia 2018, 2019; Harris et al. 2019; Raven and Wagner 2020), and light pollution (Grubisic et al. 2018). Sánchez-Bayo and Wyckhuys (2019) predict up to 40% of the world’s insect species may go extinct over the next few decades. Worldwide

**Table 2.** Number of families and species documented in the longleaf pine ecosystem, listed by order

Order	Number of families	Number of species
Amphipoda	1	1
Araneae	37	254
Astigmata	1	1
Blattodea	5	11
Callipodida	1	1
Chordeumatida	1	1
Cladocera	1	1
Coleoptera	84	643
Collembola	3	10
Copepoda	0	1
Decapoda	1	1
Dermaptera	1	1
Diptera	72	263
Embiidina	1	1
Ephemeroptera	1	1
Geophilomorpha	1	1
Hemiptera	54	140
Hymenoptera	57	692
Isopoda	3	3
Ixodida	2	7
Julida	1	1
Lepidoptera	45	681
Lithobiomorpha	2	5
Mantodea	1	4
Mecoptera	3	4
Mesostigmata	5	13
Microcoryphia	1	1
Neuroptera	8	14
Odonata	5	5
Opiliones	4	11
Orthoptera	10	165
Phasmida	3	4
Plecoptera	1	1
Polydesmida	4	5
Polyxenida	1	1
Prostigmata	2	2
Pseudoscorpiones	7	8
Psocodea	6	12
Sarcoptiformes	14	21
Scolopendromorpha	4	5
Scorpiones	2	2
Siphonaptera	5	6
Solifugae	1	1
Spirobolida	1	3
Strepsiptera	1	1
Thysanoptera	2	3
Trichoptera	1	1
Trombidiformes	5	17
Uropygi	1	1
Zoraptera	1	1
Zygentoma	1	2

See [Supp Table 1 \(online only\)](#) for complete list of species and [Supp Table 2 \(online only\)](#) for complete list of records by publication.

declines are reviewed in [Potts et al. \(2010\)](#), [Sánchez-Bayo and Wyckhuys \(2019\)](#), [Eggleton \(2020\)](#), and [Wagner \(2020\)](#).

However, other long-term studies have shown no or modest (or at least complex) declines including lepidopterans in Ecuador and Arizona, USA ([Wagner et al. 2021](#)), canopy arthropods in Puerto Rico ([Schowalter et al. 2021](#)), and insects across the United States ([Crossley et al. 2020](#)). In the LLPE, most of these declines would

seem to be due to the sensitivity of insects to habitat alteration and fragmentation ([Hall and Schweitzer 1993](#)). Lack of research in arthropod biodiversity of the LLPE compounded with the dramatic loss of this ecosystem suggests numerous LLPE arthropod species will never be known to science.

## Vulnerability of Longleaf Pine Ecosystem Arthropod Populations

We know of no long-term study that has measured the occurrence and abundance of arthropods over time in the LLPE, except for an unpublished butterfly survey at the Wade Tract, Georgia, USA from 2007 to 2020 (Sally and Dean Jue, personal communication). The Federal Register currently contains no federally listed endangered or threatened species of terrestrial arthropods within the LLPE (U.S. Fish and Wildlife Service, [ecos.fws.gov](#)). However, [Noss et al. \(1995\)](#) proposed 10 species associated with the LLPE for federal listing; [Payne et al. \(2015\)](#) also identify 10 ‘high priority’ for conservation terrestrial arthropod species in Georgia’s LLPE ([Table 3](#)). Groups more cryptic than butterflies, grasshoppers, and beetles may go unrecognized. The imperiled frosted elfin butterfly *Callophrys irus* (Godart) (Lepidoptera: Lycaenidae) has been successfully translocated within the LLPE, which may be an option for reintroducing populations to areas of extirpation ([Meyer and McElveen 2021](#)).

## Arthropod Interactions

Arthropods are critical both due to their immense biomass but also the multitude of interactions in which they engage. Numerous LLPE arthropods exhibit relationships with vertebrates, including commensal, parasitic, competitive, or predator:prey. Mutually symbiotic relationships between arthropods and vertebrates exist in pine ([Francke and Villegas-Guzmán 2006](#)) and other systems ([Ashe and Timm 1987](#), [Solodovnikov and Shaw 2017](#)) but are apparently undocumented in the LLPE.

Relationships between arthropods within the LLPE are understudied but incredibly diverse. For example, the black turpentine beetle *D. terebrans* has 36 associated mites ([Munro et al. 2019](#)), many of which presumably are also found on *D. terebrans* in the LLPE. In general, arthropods may be predators, parasitoids, competitors, commensals, symbionts, and more in their interactions with other arthropods.

Examples of arthropod-plant interactions in the LLPE include pollination, seed dispersal, nutrient enrichment, herbivory ([Levey et al. 2016](#)), the introduction of pathogens, and even plant carnivory (particularly in mesic and adjacent areas; [Brewer 2006](#)), where the native Venus flytrap *Dionaea muscipula* Ellis relies on arthropods for both pollination and nutrition but manages to rarely trap its pollinators ([Youngsteadt et al. 2018](#)). We provide further examples of arthropod interactions with vertebrates, plants, and each other below.

## Role of Fire and Arthropods

Our knowledge of the impact of fire on arthropods in the LLPE contains many gaps (in their review, [Folkerts et al. 1993](#) could only find one study [[Harris and Whitcomb 1974](#)] concerning the effect of fire on arthropods on a species level), but the topic has received more attention in other frequent fire systems ([Hermann et al. 1998](#), [McCullough et al. 1998](#), [Swengel 2001](#)) as well as the LLPE (examples below). The impact of fire on arthropod communities may be of some concern in fire prescription and land management decisions. Fire can be an effective tool for controlling insect pests, pathogens

**Table 3.** Insect species associated with the LLPE designated as ‘high priority’ for conservation in Georgia (Payne et al. 2015) and proposed for federal listing (Noss et al. 1995)

Order	Family	Common name	Species	Reference
Odonata	Gomphidae	Sandhills clubtail dragonfly	<i>Gomphus parvidens carolinus</i> Carle	Noss et al. (1995)
Orthoptera	Acrididae	(None)	<i>Aptenopedes sphenarioides apalachee</i> Hebard	Payne et al. (2015)
Orthoptera	Acrididae	(None)	<i>Eotettix palustris</i> Morse	Payne et al. (2015)
Orthoptera	Acrididae	(None)	<i>Floritettix borealis</i> (Hebard)	Payne et al. (2015)
Orthoptera	Acrididae	(None)	<i>Hesperotettix floridensis</i> Morse	Payne et al. (2015)
Orthoptera	Acrididae	Shield-tailed spur-throat grasshopper	<i>Melanoplus clypeatus</i> (Scudder)	Payne et al. (2015)
Orthoptera	Acrididae	(None)	<i>Melanoplus tumidicercus</i> Hubbell	Payne et al. (2015)
Orthoptera	Gryllotalpidae	Prairie mole cricket	<i>Gryllotalpa major</i> Saussure	Noss et al. (1995)
Coleoptera	Geotrupidae	(None)	<i>Mycotrupes cartwrighti</i> Olson & Hubbell	Payne et al. (2015)
Coleoptera	Scarabaeidae	Aphodius tortoise commensal scarab beetle	<i>Alloblackburneus troglodytes</i> (Hubbard)	Noss et al. (1995)
Coleoptera	Scarabaeidae	Copris tortoise commensal scarab beetle	<i>Copris gopheri</i> Hubbard	Noss et al. (1995)
Coleoptera	Scarabaeidae	Spiny Florida sandhill scarab beetle	<i>Gronocarus autumnalis</i> Schaeffer	Noss et al. (1995)
Coleoptera	Scarabaeidae	(None)	<i>Onthophagus polyphemus</i> Hubbard	Noss et al. (1995)
Lepidoptera	Hesperiidae	Dusky roadside-skipper	<i>Amblyscirtes alternata</i> (Grote & Robinson)	Payne et al. (2015)
Lepidoptera	Hesperiidae	Arogos skipper	<i>Atrytone arogos arogos</i> Boisduval & LeConte	Noss et al. (1995), Payne et al. (2015)
Lepidoptera	Hesperiidae	Mottled duskywing	<i>Erynnis martialis</i> (Scudder)	Payne et al. (2015)
Lepidoptera	Noctuidae	Bucholz’s dart moth	<i>Agrotis buchholzi</i> (Barnes & Benjamin)	Noss et al. (1995)
Lepidoptera	Noctuidae	Carter’s noctuid moth	<i>Photodes carterae</i> (Schweitzer)	Noss et al. (1995)
Lepidoptera	Nymphalidae	Mitchell’s satyr	<i>Neonympha mitchellii francisci</i> Parshall & Kral	Noss et al. (1995)

(Komarek 1970), and ectoparasites (Stoddard 1957, Barnard 1986). At the same time, moderation in the application of fire is advocated in some prairie ecosystems where fire sensitive insect species occur, especially rare arthropods (Opler 1981, Moffat and McPhillips 1993, Hanberry et al. 2020). It is likely important in the LLPE to consider temporal, spatial, and taxonomic resolution when examining the impact of fire on arthropods. Folkerts et al. (1993) recommend that future studies on arthropods and fire in the LLPE include several sampling methods, monthly sampling (including preburn and immediate postburn), correlated vegetation sampling, recordings of burning temperatures, litter and soil characteristics, and collection of climate data. There are of course multiple measurements of arthropods such as abundance, species richness, biomass, and community composition.

### The Impacts of Fire on Arthropods

The benefits of fire to arthropods are similar to those for the many other organisms that have evolved within the LLPE: increased biomass and diversity of the herbaceous layer, landscape heterogeneity, negative impact on competitors, burned substrate for growth of fungi (consumed by insects), weakening of host trees, favorable microclimatic conditions, and more (Folkerts et al. 1993, Wikars 1997). Costs of fire to arthropods can include direct mortality (especially flightless and relatively immobile arthropods), temporary reductions in vegetative biomass and diversity, less structural diversity for evading predators, and positive impact on competitors, all of which are usually most critical in the short time scale. These relationships may further be complicated by varying burn regimes (e.g., burns may occur annually, biennially, or less often). Survival strategies of arthropods in fire-dominant ecosystems may include the production of high population numbers (i.e., *r*-selection) which allow a species to experience high mortality in an area but recolonize from unburned refugia (Carrel 2008) and seek refuge in the soil (Cane and Neff 2011), leaf litter, or other forest strata (see below).

Temporal and spatial aspects of prescribed burns may further complicate ecological impacts on arthropods (Mason and Lashley 2021), as well as land history (Stuhler and Orrock 2016), logging activity (Campbell et al. 2007), wind disturbance (Provencher et al. 2001), beetle outbreak history (Schowalter et al. 1981), and herbicide use (Campbell et al. 2007).

### The Benefits of Pyrodiversity

Prescribed fire is undoubtedly a critical component of the modern LLPE forest structure, (Lemon 1949, Gilliam and Platt 1999), plant diversity (Kirkman and Giencke 2017, Kirkman et al. 2017), and wildlife management (Landers 1987, Smith et al. 2017). It is arguably the most important tool land managers have for maintaining the model landscape by reducing competition from hardwood trees and providing clear soil for germination of seeds of LLP and a host of other plant species. Likewise, the effectiveness of low intensity fires in reducing fuel accumulation and encouraging a diverse understory is crucial to arthropod diversity at large in the LLPE (Provencher et al. 2001, 2003; Nighohossian 2014). Yet fire is not invariably beneficial to arthropod communities.

The role pyrodiversity plays in arthropod community health is poorly studied but critical. In terms of general ecosystem functionality, some encourage promoting a heterogeneous landscape in the LLPE through a diversity of fire regimes, including variation in frequency, season, application method, and fire weather conditions (Lashley et al. 2013, Loudermilk et al. 2017). Several authors encourage pyrodiversity for the spatial and temporal refugia it provides (Hanula and Wade 2003, Knight and Holt 2005, New 2014, Chitwood et al. 2017). Burn season may affect general arthropod abundance in other systems (Johnson et al. 2008). These effects in the LLPE are further explored in the Herbaceous Layer section but are generally understudied.

Where species level interactions are examined, most studies in the LLPE demonstrate responses specific to individual species, even congeners. This makes broad taxon or guild generalizations difficult, or

at least complex. For an LLPE example, wood-nesting and ground-nesting bees are most abundant in unburned sites, sand and floral specialist bees are most abundant the same year of a burn, and nest parasites are most abundant in sites burned the previous year (Moylett 2014). Additional specific examples are found below.

In numerous systems, many arthropod taxa decline in abundance shortly after fire (Swengel 2001, Coleman and Rieske 2006, Bellanceau 2007). The diversity of most arthropod orders in the LLPE declines shortly after a fire but quickly recovers by 1 yr post-burn (O'Brien 2017). Still other studies have reported no or little short-term impacts of fire on general arthropod abundance or biomass for several nocturnal insect orders (Armitage and Ober 2012), beetles (Chitwood et al. 2017), or hymenopterans (Chitwood et al. 2017) in the LLPE. In general, however, the majority of LLPE studies indicate that more frequent fires result in higher species richness for bees (Breland 2015, Moylett et al. 2020), saproxylic insects (Campbell et al. 2008), and arthropods at large (Provencher et al. 2003, O'Brien 2017).

### Arthropods by Forest Structure

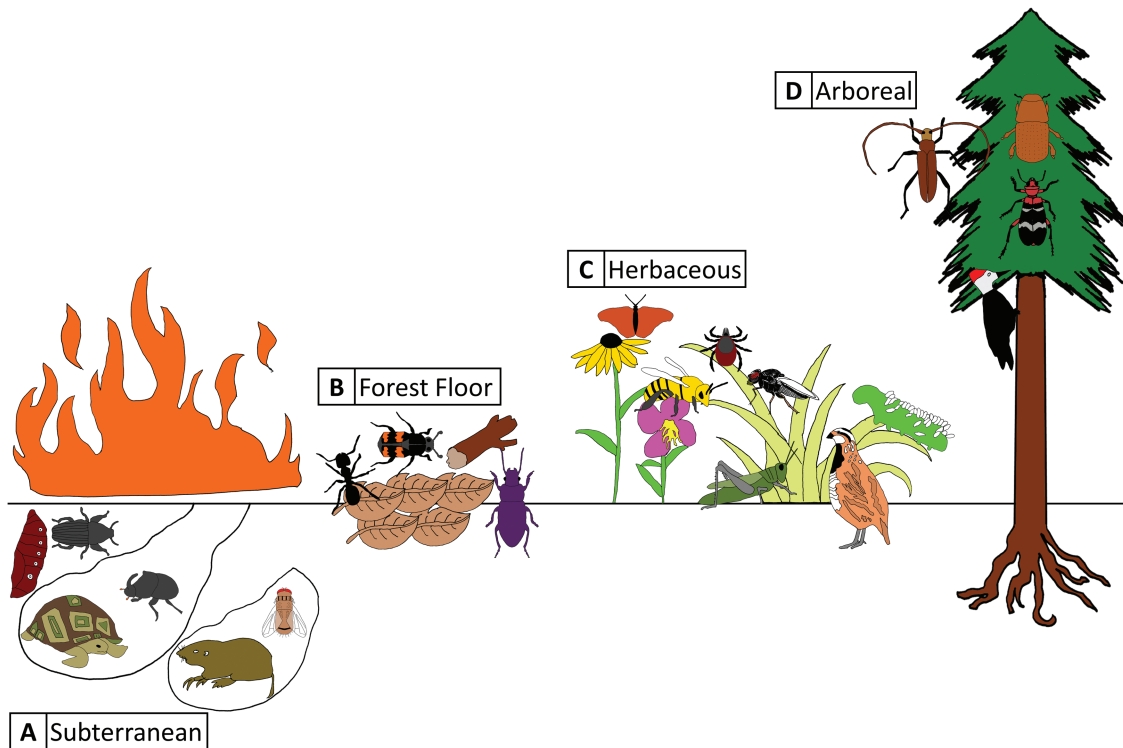
Ants of the LLPE generally fall into one of three categories: subterranean, ground-foraging, and arboreal (Lubertazzi and Tschinkel 2003), possibly four if one includes an additional herbaceous category (Van Pelt 1956, 1958). We have organized the remainder of this paper to examine all arthropods through the lens of four categories of forest structure: subterranean (edaphic), forest floor (litter), herbaceous (understory), and arboreal (trees; Fig. 3). These vertical divisions of a forested ecosystem are also logical and significant in the context of prescribed fire. Of course, life rarely fits neatly

into categories—an individual arthropod may occupy multiple structures through the course of its lifetime. We will work our way from the ground up to examine arthropods as they exist and are impacted by fire in the 1) subterranean, 2) forest floor, 3) herbaceous, and 4) arboreal strata of the LLPE.

### Subterranean

Within the soils of the LLPE, impacts from frequent fires are likely minimal to arthropods. Many may survive fire via behavioral adaptations, such as sheltering underground (Whitford and Gentry 1981, Andersen and Yen 1985, Thom et al. 2015, Simmons and Bossart 2020). Some root-feeding insect communities are more abundant and diverse in unburned sites than burned (Hanula et al. 2002, Dittler 2013), while others, such as *Hylastes salebrosus* Eichhoff, *Hylastes tenuis* Eichhoff, and *Pachylobius picivorus* (Germar), may increase after fires (Hanula et al. 2002, Sullivan et al. 2003). Still, other studies have reported no or little short-term impacts of fire on arthropods, such as subterranean termites (Isoptera: Rhinotermitidae) (Hanula et al. 2012). Ground-nesting bees may be most abundant in unburned sites, with sand and floral specialist bees most abundant the same year of a burn (Moylett 2014). Ground-nesting bee abundance and richness were significantly higher for frequently burned plots in a similar open pine system, however (Ulyshen et al. 2021b).

Growing-season fires may benefit insect conservation, occurring when adult insects are mobile or safely pupating (Hermann et al. 1998). For example, the rare, and listed as 'vulnerable,' frosted elfin butterfly *C. irus* occurs in the LLPE (McElveen et al. 2020) and likely survives fire while pupating in the soil (Thom et al. 2015). Numerous other insects pupate in the soil but live the rest of their life



**Fig. 3.** Arthropods of the longleaf pine ecosystem can be organized by forest structure. The subterranean stratum (A) includes gopher tortoise and pocket gopher commensals, root-feeders, and insects that pupate in the soil. The forest floor (B) contains epigeic predators, necrophagous arthropods, and those that dwell in leaf litter and coarse woody debris. The herbaceous layer (C) includes pollinators, herbivorous insects, parasitoids, quail prey, and ectoparasites. The arboreal stratum (D) contains prey of the red-cockaded woodpecker, pests, saproxylic insects, and their predators.

cycle above ground (other lepidopterans, beetles, and flies, including eye gnats, discussed in the Herbaceous Layer section). However, we found few studies addressing this aspect of insects of the LLPE.

In this stratum we encounter commensals of two key species in the LLPE. Gopher tortoises *Gopherus polyphemus* Daudin and southeastern pocket gophers *Geomys pinetis* Rafinesque (hereafter, pocket gophers) are belowground engineers in this system (Kinlaw and Grasmueck 2011, Catano and Stout 2015), and their burrows are home to many commensals. Other arthropods below ground include subterranean ants, termites, root infesting beetles (Zanzot et al. 2010), and insects that pupate in the soil. More than 60 vertebrate species use gopher tortoise burrows as a refuge from fire, extreme weather, desiccation, or predators (Douglass and Layne 1978, Lips 1991, Dziadzio and Smith 2016). The abundance and diversity of arthropods present in gopher tortoise burrows attracts insectivorous vertebrates (Witz et al. 1991, Knapp et al. 2018). After a gopher tortoise creates a burrow, Florida mice and other rodents dig additional, smaller burrows; this is followed by even smaller burrows excavated by arthropods, such as camel crickets *Ceuthophilus* spp. (Kinlaw and Grasmueck 2011). Hubbard (1894) was the first to detail the arthropod commensals of the gopher tortoise burrow, including the description of several species new to science at the time, listing 13 species, adding seven more species in an additional note 2 yr later (Hubbard 1896). Except for Young and Goff (1939) and some gopher tortoise tick reports (Bishopp and Trembley 1945, Clements 1956, Cooney and Hays 1972a), this fauna received little attention until the 1980s (Woodruff 1982; Milstrey 1986, 1987; Davis and Milstrey 1988). In their review, Jackson and Milstrey (1989) list 297 arthropod species associated with gopher tortoise burrows. Since 1989, there have been numerous studies conducted that involve surveys of arthropod associates of gopher tortoise burrows (Lago 1991, Alexy et al. 2003, Almquist 2017, Martinet 2017, Hipps 2019), cascading effects of its role as an ecosystem engineer (Kinlaw and Grasmueck 2011), and the role of fire ants on burrow commensal communities (Epperson et al. 2021).

Arthropod associates include those that eat tortoise dung (Milstrey 1986), predators of other arthropods (Milstrey 1986), parasites (discussed below), scavengers, and those seeking refuge from fire and desiccation. Folkerts et al. (1993) identify 16 of the gopher tortoise-associated arthropods as only occurring in tortoise burrows (obligate associates), although this is likely incomplete as any given burrow hosts only a fraction of commensal or obligate species that might exist in the gopher tortoise range. Notable associated species include dung beetles *Onthophagus polyphemi polyphemi* Hubbard, *Alloblackburneus troglodytes* (Hubbard), and *Copris gopheri* Hubbard, the gopher tortoise hister beetle *Chelyoxenus xerobatis* Hubbard, a robber fly *Machimus polyphemi* Bullington & Beck, the gopher tortoise burrow fly *Eutrichota gopheri* (Johnson) (Diptera: Anthomyiidae), and the gopher tortoise shell moth *Ceratophaga vicinella* Dietz (Lepidoptera: Tineidae) that bores into dead tortoise shells, apparently exclusively (Deyrup et al. 2005, Stillwaugh 2006). Ground-nesting bees collected at the entrances of burrows include *Hoplitis* spp., *Agapostemon* spp., and *Augochlora pura* (Hipps 2019). The Africanized honey bee *Apis mellifera* L. has also been recorded in gopher tortoise burrows (Kern 2007).

Although Hubbard (1894) completely excavated burrows to catalog arthropod associates, less intrusive techniques now exist. Hipps (2019) tested several methods of collecting arthropod burrow associates, such as pitfall traps at burrow aprons, soil sampling, UV light sheets, dung baiting, and the burrow façade trap or ‘Wile E. Coyote trap’ as described by Almquist (2017). As is common for arthropod sampling in general, a variety of methods is necessary to

gain a more complete representation of the fauna. Carbon dioxide bait traps for animal burrows could serve well in the LLPE for both gopher tortoise and pocket gopher parasites (Miles 1968, Adeyeye and Butler 1990).

The gopher tortoise tick, *Amblyomma tuberculatum* Marx (Acari: Ixodidae), most commonly parasitizes the gopher tortoise, but the larval form can use a variety of other vertebrate hosts (Bishopp and Trembley 1945, Milstrey 1986) including, in isolated instances, humans (Goddard 2002). The adult tick feeds exclusively on the gopher tortoise. However, because immatures can feed on a variety of mobile vertebrates—such as birds—they can spread to previously tick-free tortoise populations (Wilson and Durden 2003). This tick is likely the largest in North America (Cooney and Hays 1972a) and perhaps the second largest known in the world (Bishopp and Trembley 1945). Like other tick species, *A. tuberculatum* hosts pathogens such as *Rickettsia* and others (Zemtsova et al. 2012, Budachetri et al. 2016, Crosby et al. 2021, Page-Karjian et al. 2021). This species may prove beneficial as well, however: the transcriptome of this tick’s salivary glands may be of pharmacological use for hemostasis and antiinflammation (Karim et al. 2021). Ennen and Qualls (2011) found *A. tuberculatum* at 23% of gopher tortoise populations in southern Mississippi, USA; this relatively low proportion is likely influenced by environmental factors such as sand depth, percentage of topsoil, and burrow apron sand composition. Cooney and Hays (1972b) collected as many as 19 ticks from an individual gopher tortoise. *Ornithodoros turicata* (Dugès) (Acari: Argasidae) also parasitize gopher tortoises (Milstrey 1987; Adeyeye and Butler 1989, 1990), as does the turtle generalist flesh fly *Cistudinomyia cistudinis* (Aldrich) (Diptera: Sarcophagidae) (Knipling 1937, Johnson and Milstrey 1989).

The invasive fire ant has been documented to negatively impact both gopher tortoises (Epperson and Heise 2003; Dziadzio et al. 2015, 2016) and the arthropod commensals that live in their burrows (Wetterer and Moore 2005, Epperson et al. 2021).

Like gopher tortoises, pocket gophers provide shelter for animals with their burrows, aerate soil, and impact plant communities through their behavior (Kalisz and Stone 1984, Reichman and Seabloom 2002, Pynne 2020). They have been called both a keystone species (Skelley and Kovarik 2001) and ecosystem engineer by some (Reichman and Seabloom 2002, Duncan et al. 2020, Pynne 2020), as well as a ‘homely, belligerent sausage’ (Avisé and Laerm 1982). We found no reports of pocket gopher arthropod commensals before 1939. This is likely due to the challenges of accessing the burrows, which can be up to 1 m deep and lack obvious surface openings like the gopher tortoise burrow; trapping arthropods was determined to be significantly less laborious (Hubbell and Goff 1939). Sampling for associated arthropods requires trapping and removing the pocket gopher, as they will quickly bury any arthropod trap and plug up any holes made by researchers (Gates et al. 1988, Connor and Risch 2009). This commensal fauna includes numerous rare and cryptic species. For example, the hister beetle *Onthophilus giganteus* Helava was known from a single specimen that got damaged en route to a museum, until targeted trapping resulted in dozens of specimens (Skelley and Kovarik 2001). Similarly, all members of the scarab genus *Stephanucha* are considered rare but sifting through pocket gopher mounds produced 50 adults (Skelley 1991). Intensive trapping efforts have demonstrated burrow arthropod activity to peak during the winter months (Skelley and Gordon 2001). More than 60 species of arthropods are associated with pocket gopher burrows (Hubbell and Goff 1939, Means 2006). Many of these resemble cave-dwelling organisms in that they have a pale color, reduced eyes, reduced wings, and elongated appendages (Skelley and Gordon 2001). Some



notable arthropods include the camel cricket *Typhlocyba floridanus* Hubbell (Hubbell and Goff 1939, Hubbell 1940, Skelley and Gordon 2001), various hisster beetles (Ross 1940), scarab beetles (Cartwright 1939; Skelley 1991; Skelley and Woodruff 1991; Skelley and Gordon 1995, 2001), rove beetles (Coleoptera: Staphylinidae) (Hubbell and Goff 1939, Skelley and Gordon 2001), small carrion beetles (Coleoptera: Leiodidae: Cholevinae) (Peck and Skelley 2001), flies (Hubbell and Goff 1939, Skelley and Gordon 2001), centipedes (Chamberlin 1940), and other minute arthropods such as mites and collembolans (Hubbell and Goff 1939).

The camel cricket *T. floridanus* has not been collected above ground and is thought to never come to the surface (Skelley and Gordon 2001). Other associates have though, such as scarab beetles, which may find mounds using chemical, visual, thermal, and water content cues (Skelley and Gordon 2001). Pocket gophers inadvertently provide food to arthropods by exposing roots, stems, bulbs, mycelia, feces, and decomposing vegetation as they feed and burrow. The arthropods, as consumers of these materials, are in turn consumed by predators and decomposers (Hubbell and Goff 1939). Some arthropods can live for a period of time after a gopher leaves, but the burrow may collapse without maintenance (Hubbell and Goff 1939). Red-tailed skinks *Eumeces egregius* (Baird) bask on mounds created by earth-boring scarab beetles (Coleoptera: Geotrupidae), as well as occasionally on mounds made by gopher tortoises and pocket gophers (Mount 1963).

Ectoparasites of the pocket gopher include mites (Hubbell and Goff 1939, Whitaker and Wilson 1974), fleas (Hubbell and Goff 1939, Layne 1971), lice (Hubbell and Goff 1939, Price and Timm 1979, Wilson and Durden 2003), and ticks (Hubbell and Goff 1939). The flea *Foxella ignota* (Baker) commonly parasitizes *Geomys* spp. and the closely related *Thomomys* spp. in western North America but has not been documented on *G. pinetis* (Hubbell and Goff 1939, Layne 1971).

Thief ants (*Solenopsis* spp.) dominate subterranean ant collection efforts in the LLPE, comprising as much as 70–98% of the subterranean ant abundance (Lubertazzi and Tschinkel 2003, Sells et al. 2015, Ohyama et al. 2020b). These ants consume the brood of other ant species (Thompson 1989, Ohyama et al. 2020b) and rarely appear above ground (King and Porter 2005). Along with spiders and beetles, ants create soil disturbances in the LLPE (Hermann 1993, Simkin and Michener 2005). *Solenopsis molesta* (Say) did not respond to both experimental and natural warming (Resasco et al. 2014b). For other reports of subterranean ants, see [Supp Table 1 \(online only\)](#).

Numerous casts of ant nests have been created in the LLPE (methods described in Tschinkel 2010). Species examined include *Formica pallidefulva* Latreille (Mikheyev and Tschinkel 2004), *Pogonomyrmex badius* (Latreille) (Tschinkel 2004), *Camponotus socius* Roger (Tschinkel 2005), *Odontomachus brunneus* (Patton) (Cerquera and Tschinkel 2010), *Aphaenogaster floridana* Smith, *A. treatae* Forel, and *A. ashmeadi* (Mayr) (Tschinkel 2011), and *Pheidole morrisii* Forel (Murdock and Tschinkel 2015). These groundbreaking studies lend crucial information to understand nest architecture, ant natural history, and social structure.

## Forest Floor

The forest floor is home to epigeic predators and foragers (particularly dominated by ants, ground beetles, and spiders) and necrophagous arthropods, as well as those that dwell in leaf litter and coarse woody debris. Although complex, fire plays a relatively more important role in arthropod communities at this layer compared to below ground. Some studies showed an increase in abundance

following a burn on a relatively short time scale for dolichoderine ants (Izhaki et al. 2003), springtails (Provencher et al. 1998a), and spiders (Chitwood et al. 2017), yet others demonstrated more leaf litter arthropods in unburned areas compared to burned areas (Heyward and Tissot 1936, Eady and Conn 2004).

Some studies have shown no difference in species richness in ants and termites by fire regime (LaRussa and Scholtens 2015, Atchison et al. 2018) or genera richness in ground-dwelling arthropods (Hanula and Wade 2003). The ground-hunting spider *Ctenus hibernalis* Hentz (Araneae: Ctenidae) showed no difference in abundance between burned and fire-suppressed areas but did have higher average body mass in the burned areas (Cole and Hataway 2016). No or little short-term impacts of fire on abundance or biomass were demonstrated in ground beetles (McCoy 1987, Colby 2002) and total litter arthropods (New and Hanula 1998, Bellanceau 2007).

Fire did not affect species richness of leaf litter arthropods (e.g., ants and termites) but did affect species composition (Atchison et al. 2018). Species richness did not differ by treatment (plots that were burned on 1-, 2-, 3-, 30-, and 75-yr cycles), but ant community composition and species density did differ between the 1-, 2-, and 3-yr burn cycles, and the 30- and 75-yr burn cycles (Atchison et al. 2018).

Fire can induce species-specific responses for ground-dwelling arthropods (McCoy and Kaiser 1990, Hanula and Wade 2003, Izhaki et al. 2003, Atchison et al. 2018). Six ground beetle species (Coleoptera: Carabidae) were more numerous than other species in fire excluded areas where leaf litter was present (Harris and Whitcomb 1974). Two species *Notiophilus novemstriatus* LeConte and *Pasimachus sublaevis* Palisot de Beauvois were found in greater numbers where forests were burned annually, however. This species-specific response has been observed in other systems as well (Cobb et al. 2007). Working in longleaf pine flatwoods in Central Florida, Atchison et al. (2018) found higher abundance of exotic ants in frequently burned sites compared to a plot that had not been burned in 75 yr, in which they detected only native species.

There have also been different responses by guild for ants (Izhaki et al. 2003). For example, the high noon ant *Forelius pruinosus* (Roger) exhibited large increases in abundance after fire, outcompeting other groups. However, by 6 mo post-fire, the high noon ant numbers had decreased, and other groups had recovered (Izhaki et al. 2003).

We address the relatively low-diversity subterranean, herbaceous, and arboreal ants (Lubertazzi and Tschinkel 2003) in their appropriate sections, but ground-foraging ants represent the bulk of ant diversity—and ant research—in the LLPE. Species collected in large numbers include *Aphaenogaster treatae*, *A. fulva* Roger, *Odontomachus brunneus*, *Pheidole dentata* Mayr, *P. morrisii*, and the fire ant. Counter to patterns of biodiversity seen in other arthropods, ant species richness may be negatively correlated with ground cover (Whitford and Gentry 1981, Lubertazzi and Tschinkel 2003, Graham et al. 2004). Ant communities also differ between habitat types (e.g., sand hills vs. flatwoods) (Ohyama et al. 2018) and season (Tschinkel 1987).

The fire ant may cause devastating declines in native ant and other arthropod populations, particularly in the southeastern United States (Porter and Savignano 1990, Gotelli and Arnett 2000, Haines 2018). They often dominate ant collecting efforts where they are present in the LLPE, comprising as high as 97% of ants captured (Colby and Prowell 2006, Sells et al. 2015). In the LLPE, their abundance is often negatively correlated with biomass, abundance, and species richness of other arthropods—especially native ants (Landry 2004, Epperson and Allen 2010, Resasco et al. 2014a, Haines 2018), but the relationship can be complex (Stuble et al. 2009, Cumberland and Kirkman 2012). Other studies have shown the fire ant to coexist with

native ant populations in the LLPE (Colby 2002; King and Tschinkel 2006, 2013a). In a different system, ant communities affected by the fire ant return essentially to preinvasion levels given enough time (Morrison 2002, Tschinkel and King 2013). Fire ant populations were experimentally reduced by a specific granular pesticide, but this reduction did not increase native ant richness (Roeder et al. 2021). In the LLPE, human-caused disturbance may play a larger role in disrupting native ant populations than fire ants, which may be more ‘passengers’ than ‘drivers’ of ecological impact (King and Tschinkel 2006, 2008, 2013a). However, these conclusions have drawn criticism (Stuble et al. 2013), a rebuttal (King and Tschinkel 2013b), and a summary of the disagreement (Hill et al. 2013). Other exotic ant species do not seem to displace native ant species (Ohyama et al. 2020a).

The fire ant can be beneficial in reducing horn flies, lone star ticks, and agricultural pests of cotton and sugar cane (Tschinkel 1993). They may also be parasitized by mermithid nematodes in the LLPE (McInnes and Tschinkel 1996). Native ants favor drier conditions than fire ants (Stuble et al. 2009). For example, in North Florida, the fire ant and its native congener *S. geminata* (Fabricius) barely overlap in distribution, with the fire ant limited to heavily disturbed sites and seasonal ponds, whereas *S. geminata* is common in undisturbed LLPE (Tschinkel 1988). Despite its affinity to disturbance, the fire ant is found in areas with an abundance of disturbance-phobic wiregrass, likely due to favorable microclimate from the grass (Lubertazzi and Tschinkel 2003). Fire ant abundance is higher in disturbed areas within the LLPE (e.g., road and powerlines; Stiles and Jones 1998) and six times higher in local pastures than in the LLPE (King and Tschinkel 2006). Carroll and Hoffman (1997), however, found the fire ant as the most common ant species at both disturbed and undisturbed sites in the LLPE. It may also be only found in frequently burned areas and not in plots that were unburned for 35–75 yr (Atchison et al. 2018).

The exotic ant species *Pheidole obscurithorax* Naves was not collected in LLPE in 2004 (Storz and Tschinkel 2004), although it greatly expanded its range by 2007 (King and Tschinkel 2007) and has since been collected in the LLPE in 2012, albeit not in 2018 at the same location (Ohyama et al. 2020a).

The fungus-cultivating *Trachymyrmex septentrionalis* (McCook) is very abundant in the LLPE; a single hectare can contain over 1,000 nests, 235,000 workers, and 3.5 kg of symbiotic fungus, with the largest colonies occurring in open habitat (Seal and Tschinkel 2006). This species thrives in drought conditions, displaces at least 1 metric ton of soil/ha/yr (Seal and Tschinkel 2006, 2008, 2010), and builds a distinctive crescent-shaped mound to one side of the entrance hole. Despite their high prevalence on the landscape, these ants are not collected effectively in pitfall traps (Lubertazzi and Tschinkel 2003, King and Tschinkel 2008), demonstrating the need for a variety of trapping methods.

Studies on ant behavior in the LLPE include those on natural history of *Odontomachus brunneus* (Powell and Tschinkel 1999, Hart and Tschinkel 2012), sociometry, soil movement, and labor allocation in *P. badius* (Tschinkel 1999a,b; Smith and Tschinkel 2005, 2006, 2007; Rink et al. 2012; Kwapich and Tschinkel 2013; Tschinkel 2013, 2014, 2015), fungal substrate selection in *T. septentrionalis* (Seal and Tschinkel 2007a, 2008), colony founding in fungus-gardening ants (Seal and Tschinkel 2007b), desiccation resistance (Hood and Tschinkel 1990), dispersal (King and Tschinkel 2016), and effects of groundwater on ant distribution (Tschinkel et al. 2012). *Myrmecina americana* Emery decreased in abundance from both natural and experimental warming (Resasco et al. 2014b).

Necrophagous arthropods presumably play important roles in decomposition in the LLPE forest floor and litter layer. Documented taxa of the LLPE include blow flies (Diptera: Calliphoridae) (Barwary 2010), flesh flies (Diptera: Sarcophagidae) (Underwood 2009, Nighohossian 2014), ants (Trumbo 1990), and carrion beetles (Coleoptera: Silphidae) (Trumbo 1990, T.N.S., personal observation), among others. Very little is known about their diversity or ecological roles, aside from a study of necrophagous beetles in a mixed longleaf-loblolly forest (Silva et al. 2020). Arthropod and microbial decomposition activity is highest in warmer months in the LLPE (Turner et al. 2017). Carrion beetles are reportedly less abundant and less diverse in southeastern than northern forests (Trumbo 1990). Although ants are both important decomposers in other systems and well-studied in the LLPE, little is known of their role as decomposers in the LLPE.

Folkerts et al. (1993) found no studies of litter arthropods in the LLPE and suggest that they may be relatively unimportant due to litter consumption by fire. The most abundant arthropod groups in the LLPE collected from Berlese funnels of leaf litter are mites, ants, springtails, fly larvae, beetles, and termites (Folkerts et al. 1993). Although Folkerts et al. (1993) did not collect many millipedes from Berlese funnels, they have been reported from other trapping methods such as pitfall traps (Milstrey 1987, Corey and Stout 1992, Hanula and Wade 2003, Hanula et al. 2006).

Raking leaf litter caused an increase in abundance of multiple arthropod orders in longleaf plantations but reduced abundance in loblolly stands (Ober and Degroote 2011). Spiders, mites, and collembolans were more abundant in raked longleaf stands compared to unraked, but the opposite was true for members of Blattodea (Ober and DeGroot 2011). Raking decreased general arthropod abundance significantly in loblolly pine stands compared to longleaf, perhaps due to evolutionary adaptations to frequent disturbance such as fire (Ober and DeGroot 2011). This study only went to order; litter removal may alter trophic interactions by affecting community structure and functional groups. Atchison et al. (2018) suggest the relatively dry, nutrient-rich leaf litter of the LLPE supports ant community heterogeneity.

Dead wood, including coarse woody debris, provides important habitat and food sources to many arthropods such as termites, roaches, flies, hemipterans, and beetles (Seibold et al. 2016, Gossner and Damken 2018, Ulyshen 2018). Seibold et al. (2015) and Sandström et al. (2019) review dead wood and its importance for biodiversity.

Removal of coarse woody debris in the LLPE did not decrease general arthropod abundance but did decrease abundance for some families and overall diversity (Hanula et al. 2006). Coarse woody debris in old-growth LLPE varies widely in volume but is higher than secondary forests of the LLPE (Ulyshen et al. 2018). This is likely because heartwood—which longleaf pine trees produce in great amounts over time—decays more slowly than sapwood (Eberhardt et al. 2009, Ulyshen et al. 2018). Logs placed in annually burned plots lost significantly less mass than logs placed in unburned plots, possibly due to reduced fungal, microbial, and arthropod activity (Hanula et al. 2012).

Termites play an important role in numerous forest systems (Ulyshen 2014); the LLPE is likely no different. Termites were significantly more abundant in burned LLPE stands, compared to unburned longleaf pine and hardwoods (Gentry and Whitford 1982). Burn frequency did not affect the presence of termites in another study, likely due to seeking refuge beneath the soil (Hanula et al. 2012). Termites attacked 90% of pine blocks placed on mineral soil within 7 mo, but none placed on pine straw (Gentry and

Whitford 1982). Gentry and Whitford (1982) suggest that fire enhances wood availability to termites by speeding the contact of dead wood to soil.

## Herbaceous Layer

In the herbaceous layer, we examine pollinators, herbivorous insects, parasitoids, and general interactions of arthropods with vertebrates. Kirkman et al. (2004) found plant species richness to increase with fire frequency and soil moisture, with plant biodiversity shifting from the canopy to ground flora as fire frequency increases. The clearest and most intuitive link between fire and arthropod species richness is fire's well-documented role of increasing plant species richness in the LLPE (Kirkman et al. 2004), with links to insect abundance and richness (Izhaki et al. 2003). Fire plays the most critical role at this level of the longleaf pine forest, regulating plant diversity, arthropod diversity, and multi-trophic interactions between plants, herbivores, and parasitoids (Dell et al. 2019). More frequent fires result in higher species richness for bees (Breland 2015, Moylett et al. 2020). Some studies show an increase in abundance following a burn such as with orthopterans (Provencher et al. 1998a, Kerstyn and Stiling 1999, Bellanceau 2007), halictid bees (Campbell 2005), dance flies (Diptera: Empididae) (Provencher et al. 1998a), and planthoppers (Hemiptera: Cicadellidae, Flatidae) (Provencher et al. 1998a). In contrast, others show biomass and abundance to increase with time-since-burn for butterflies (Wiebush 2020), lepidopterans (Armitage and Ober 2012), orthopterans (Hurst 1972, Knight and Holt 2005, Chitwood et al. 2017), the palmetto tortoise beetle *Hemisphaerota cyanea* (Say) (Coleoptera: Chrysomelidae) (Mutz et al. 2017), other leaf beetles (Coleoptera: Chrysomelidae) (Provencher et al. 1998a), and northern bobwhite quail prey *Colinus virginianus* (L.) (Hurst 1970, Dunaway 1976). Other studies show no or little short-term impacts of fire on abundance and biomass for bees (Breland 2015, Simmons and Bossart 2020), leaf miners (Kerstyn and Stiling 1999), or pollinating beetles and flies (Campbell 2005).

Beyond simply surviving in a fire-dominant ecosystem, some arthropods develop adaptations to exploit recent post-fire landscapes. Although orientation towards or away from (or similar behavioral responses to) fire—for which we herein coin the term 'pyrotaxy'—have not been well-documented in the LLPE, there are numerous arthropods that directly require fire and are indeed attracted to it. In the herbaceous layer of the LLPE, red-legged grasshoppers *Melanoplus femurrubrum* (De Geer) move from unburned locations to burned locations within 1 wk of a fire (Komarek 1965). Arthropods of the LLPE may escape from fire to seek refuge in wood (Ulyshen et al. 2010, Hanula et al. 2012), climbing into the canopy (Dell et al. 2017), climbing other vegetation (Komarek 1965), flying away (Knapp et al. 2018), or recolonizing from unburned areas (Hall and Schweitzer 1993).

Positive pyrotaxy is seen in vertebrates as well. Black-backed woodpeckers arrive at burned areas within days or weeks of fire, perhaps attracted visually by smoke plumes (Stillman et al. 2021). Feral cats travel up to 12.5 km to hunt in severely burned areas (McGregor et al. 2016). Raptors intentionally spread fire in Australia by dropping burning sticks into unburned areas (Bonta et al. 2017). Negative pyrotaxy has also been documented in meadow voles (Geluso and Bragg 1986) and the Louisiana pine snake in the LLPE (Rudolph et al. 1998). Other vertebrate behavioral adaptations to fire include open-canopy specialist snakes of the LLPE using frequently burned (<2 yr) locations more often than locations with a longer burn interval (Howze and Smith 2021),

raptors using a location at a rate of seven times more frequently after it was burned (Hovick et al. 2017), and more (Nimmo et al. 2019).

In addition, for many arthropod populations [e.g., pygmy grasshoppers *Tetrix subulata* (L.) in Sweden] the frequency of melanistic individuals increases after burns, resulting in increased camouflage and increased survival (Forsman et al. 2011).

The time of year at which the land is burned has important implications for land management, including for arthropods. Prescribed fire that occurs during periods of larval feeding and development can result in mortality. For example, a population of *Speyeria idalia* (Drury) (Lepidoptera: Nymphalidae) was extirpated in prairie lands due to fire (Moffat and McPhillips 1993). Some studies suggest no effect of burn season on arthropod communities (Sisson 1991, Pavon 1995, Hiers et al. 2000) and bee richness or abundance (Bartholomew and Prowell 2006). This knowledge gap deserves more attention in the future. Responses vary by species for bees (Ulyshen et al. 2021a), ticks (Gleim et al. 2013), and presumably other taxa as well. Pyrodiversity benefits both bees and butterflies in the LLPE; the number of nearby unique burn histories was a positive indicator of species richness (Ulyshen et al. 2021a).

We found few studies on parasitoids in the LLPE. Folkerts et al. (1993) discuss parasitoids in general ecological terms, but do not cite any studies concerning parasitoids in the LLPE. Parasitoids in general span a variety of taxa within Holometabola, including several orders, but are primarily represented by members of Hymenoptera and Diptera (Eggleton and Belshaw 1992, Feener and Brown 1997). Dell et al. (2019) documented a network in the LLPE of 64 host plant species, 183 caterpillar species, and 47 parasitoid species—for a list of species see Supp Table 1 (online only). Members of the genus *Pediobius* (Hymenoptera: Eulophidae) parasitize both the economically relevant pitch moths *Dioryctria* spp. (Lepidoptera: Pyralidae) and their parasitoid *Lixophaga* spp. (Diptera: Tachinidae) (Belmont and Habeck 1983). *Hyssopus rhyacioniae* Gahan (Hymenoptera: Eulophidae) parasitizes *Dioryctria* spp. as well, averaging about 40 individuals per larva (Belmont and Habeck 1983). The parasitoid tachinid *Iceliopsis borgmeieri* Guimarães was only known in Brazil until collected in the LLPE of Florida (Stireman and Dell 2017).

In the LLPE, we have observed an undetermined tachinid fly parasitizing a monarch butterfly *Danaus plexippus* (L.) and a species of *Microdon* (Diptera: Syrphidae) near a *Camponotus floridanus* (Buckley) (Hymenoptera: Formicidae) nest. Little is known of native siricids and their parasitoids in the southeastern United States in general (Barnes et al. 2014), which is apparently the norm for many groups within the LLPE.

Generally speaking, pollinators provide a critical ecosystem service that benefits both agriculture and wild plant communities. Approximately 75% of plant species (especially rare plants) in the LLPE are pollinated by arthropods (Folkerts et al. 1993). These pollinators belong to several arthropod orders, notably Hymenoptera, Lepidoptera, Diptera, and Coleoptera. Many of them are polylectic (pollinating several plant species; Folkerts et al. 1993, Bartholomew et al. 2006), which creates a complex and intricate web of interactions. Bees (Hymenoptera: Anthophila) have dominated the field of LLPE pollinator research, likely due to their status as the most efficient pollinators (Moylett et al. 2020), but other taxa have been examined as well. Rare plants may depend on arthropod pollination in the LLPE (Pitts-Singer et al. 2002). Despite their global importance, both wild and managed pollinators face several potential threats (shared with arthropods at large) such as habitat loss, pesticides (Rundlöf et al. 2015, Brittain et al. 2010, Woodcock et al.

2017, Tsvetkov et al. 2017), climate change, and disease (Fürst et al. 2014).

Historical land use—such as agriculture and fire suppression—does not appear to tremendously affect bees in the LLPE after restoration (Breland et al. 2018, Odanaka et al. 2020). There appear to be no differences between primary and mature secondary forests for bees (Ulyshen et al. 2020). A small, restored habitat fragment of the LLPE can support a relatively large and diverse pollinator community (Bartholomew and Prowell 2006, Bennington and May 2020). These conclusions may be confounded by a disconnect between where bees forage and where they nest, as most bee studies capture foraging bees.

Restoration thinning in the LLPE increases bee abundance, richness, and diversity (Breland et al. 2018, Odanaka et al. 2020). Indeed, it has been well demonstrated in multiple conifer systems that bee abundance and richness increase as basal area decreases (Taki et al. 2010; Hanula et al. 2015, 2016; Rhoades et al. 2018; Ulyshen et al. 2021a), even to the point that forest canopy reductions due to a bark beetle outbreak significantly increased bee abundance and diversity (Davis et al. 2020, Foote et al. 2020). Upland sites contain higher bee abundance and species richness than flatwood sites (Bartholomew and Prowell 2006).

Bee indicator species of thinned LLPE may include: *Anthidiellum n. notatum* (Latreille), *Apis mellifera*, *Hoplitis truncata* (Cresson), *Lasioglossum apokense* (Robertson), *Lasioglossum imitatum* (Smith), *Lasioglossum nymphale* (Smith), *Lasioglossum trigeminum* Gibbs, *Megachile georgica* Cresson, *Megachile mendica* Cresson, *Megachile petulans* Cresson, *Megachile texana* Cresson, and *Melissodes boltoniae* Robertson, compared to unthinned LLPE: *Lasioglossum bruneri* (Crawford) and *Lasioglossum raleighense* (Mitchell) (Breland et al. 2018). Members of the genus *Lasioglossum* often dominate collecting efforts in the LLPE, comprising up to nearly half of individuals at some sites (Hall and Ascher 2014; Breland 2015; Miljanic et al. 2019; Moylett et al. 2020; Ulyshen et al. 2020, 2021a). Generally, fire improves bee species richness and abundance (Breland 2015, Moylett et al. 2020) or at least has no negative effect (Simmons and Bossart 2020). This is especially the case when fire regimes incorporate a high amount of pyrodiversity (Ulyshen et al. 2021a). The benefit of fire is likely due to the role it plays in promoting open habitat with rich floral resources (Moylett et al. 2020).

Both the abundance and diversity of pollinators represented in collecting efforts are affected by trap type and color (Bartholomew and Prowell 2005, Campbell and Hanula 2007, Orfinger et al. 2017), as well as the use of supplemental netting (Bartholomew et al. 2006, Roulston et al. 2007, Hall and Ascher 2014). In the open habitat of the LLPE, camera traps may be an effective tool to monitor butterflies, such as the rare frosted elfin *Callophrys irus* (Godart) (McElveen and Meyer 2020).

Surveys and species compilations involving the LLPE have been conducted for bees in Florida (Hall and Ascher 2014), Louisiana, USA (Bartholomew et al. 2006, Owens et al. 2018), and Mississippi (Michener 1947, Bartholomew et al. 2006), as well as moths and butterflies in North Carolina, USA (Hall and Schweitzer 1993) and Louisiana (Landau and Prowell 1999, Prowell 2001). For a list of pollinator species, see Supp Table 1 (online only). Pollinator reviews include those that inhabit managed conifer forests (Rivers et al. 2018) and the southeastern United States (Hanula et al. 2015, 2016).

Fire ants likely negatively affect native herbaceous flora of the LLPE by displacing native arthropods responsible for pollination and seed dispersal (Lubertazzi and Tschinkel 2003). These ants dominate seed movement in the LLPE but do not appear to increase

germination rates (Cumberland and Kirkman 2013). Other species move seeds as well (Stuble et al. 2010), but fire ants were responsible for more than half of all seed removals (Stuble et al. 2010). Fire ants also collected more elaiosome-bearing than nonelaiosome-bearing seeds (Cumberland and Kirkman 2013). They may also increase soil nutrients, particularly  $\text{NH}_4^+$ , significantly enhancing plant growth (Lafleur et al. 2005). Harvester ants *P. badius* in the LLPE dispersed seeds further than explosively dispersing plants did via ballistics (Stamp and Lucas 1990). *Dolichoderus mariae* Forel ants construct nests at the base of wiregrass and tend aphids and scale insects for honeydew on herbaceous vegetation (Laskis and Tschinkel 2009).

Virtually all terrestrial vertebrates in the LLPE host ectoparasites, most of which are arthropods. It is worth mentioning that likely most are not specific to the LLPE. These may include mosquitoes (Buckner et al. 2011), bot flies (technically endoparasites) (Clark and Durden 2002, Nims et al. 2008), keds (Diptera: Hippoboscidae) (Martin 2012, T.N.S., personal observation), horse flies (Blickle 1959, Schreck et al. 1993), fleas (Durden et al. 2000, Pung et al. 2000b, Clark and Durden 2002, Nims 2005, Nims et al. 2008), lice (Durden et al. 2000, Pung et al. 2000b, Clark and Durden 2002, Nims 2005, Nims et al. 2008), ticks (Durden et al. 2000; Rogers 1953; Pung et al. 2000b; Clark and Durden 2002; Nims et al. 2008; Gleim et al. 2013, 2014, 2019), chiggers (Folkerts et al. 1993, Durden et al. 2000, Pung et al. 2000b, Nims et al. 2008, Williams 2010), and other mites (Pung et al. 2000b; Clark and Durden 2002; Nims et al. 2004, 2008; Nims 2005).

Nims (2005) provides the most thorough study to date of small mammal ectoparasites in the LLPE, including several new host-ectoparasite associations. Fire is considered an effective tool in decreasing abundance of ticks (Rogers 1953; Davidson et al. 1994; Gleim et al. 2013, 2014, 2019), chiggers (in loblolly pine, Pearse 1943), and ectoparasites in general (Nims 2005, Scasta 2015).

The eye gnat *Lihippelates pusio* (Loew) (Diptera: Chloropidae) and its congeners are prevalent in agriculture but less studied in and around the LLPE (Bigham 1941, Gerhardt and Axtell 1972, Provencher et al. 1998b) where they are ubiquitous and very abundant on the landscape (T.N.S., personal observation). They are considered a pest of humans, livestock, and domestic pets (Herms 1928, Herms and Burgess 1930, Day and Sjogren 1994). Despite their prevalence and likely ecological importance in the LLPE, there is currently no research on eye gnats in this system.

Several dozens of bird species inhabit the LLPE, such as northern bobwhite quail, red-cockaded woodpecker, white-breasted nuthatch *Sitta carolinensis* Latham, brown-headed nuthatch *Sitta pusilla* Latham, and Bachman's sparrow *Peucaea aestivalis* (Lichtenstein) (Means 2006). Numerous insectivorous birds certainly have considerable effects on arthropod populations through various methods of predation (Means 2006). Insects and birds can interact in more indirect ways as well, such as sparrows benefitting from openings caused by insect infestations (Carrie et al. 2002). However, little research has been devoted to disentangling these complex interactions.

Arthropods are important food items for several other LLPE vertebrates too, such as flying squirrels (Harlow and Doyle 1990), bats (Means 2006), Bachman's sparrow *Peucaea aestivalis* (Lichtenstein) (Mitchell 1998), lizards (Guyer and Bailey 1993, Williams and McBrayer 2015), wild turkey *Meleagris gallopavo* L. (Chitwood et al. 2017), small mammals, salamanders (Guyer and Bailey 1993), frogs (Guyer and Bailey 1993), and certainly dozens of other species. The gopher tortoise primarily consumes vegetation but is reported to consume arthropods; as many as 75% of scat samples may contain insect parts (MacDonald and Mushinsky 1988). It is not known whether these records represent accidental or intentional

consumption of arthropods. Research on the consumption of arthropods by other vertebrate species is lacking for the LLPE. The exceptions are red-cockaded woodpeckers and quail, which are of considerable management concern. Conservation activities for these two species are significant aspects of efforts to preserve the LLPE (Kirkman and Jack 2017).

The bobwhite quail's range extends beyond that of longleaf pine, but historically it primarily lived in the LLPE due to its characteristic open canopied habitat. Much of our current understanding of the role fire plays in the LLPE is attributed to the bobwhite quail decline seen in the 1920s (Means 2006). This ecologically and economically important game bird (Burger 2002, Johnson and Gjerstad 2006, Johnson et al. 2012, Butler et al. 2017) feeds heavily on LLP seed, especially in winter months (Reid and Goodrum 1979).

Arthropods are particularly important to young quail chicks (Stoddard 1931, Stoddard 1957, Hurst 1972) and females (Brennan and Hurst 1995). They can comprise as high as 41% of crop volume in summer months and 20% in autumn, though this falls to <5% during the winter (Reid and Goodrum 1979). Simply measuring arthropod abundance and biomass in areas where quail occur does not translate to understanding their diet, as these birds do not randomly consume arthropods (Hurst 1972, Palmer et al. 2001). Instead, arthropod fragments from feces and euthanized gamebirds can be identified to provide direct information of prey items (Moreby 1987, Butler et al. 2004). In the LLPE, arthropods often consumed by quail include beetles, leafhoppers, other true bugs, spiders, grasshoppers, ants, ticks, and other small arthropods (Hurst 1972, Reid and Goodrum 1979, Patterson and Knapp 2018), although grasshoppers are not eaten in amounts proportional to their relative abundance and biomass (Hurst 1972).

Large LLP seed mast events are positively correlated with quail population increases and negatively correlated with Lyme disease, presumably due to large quail populations consuming ticks (Patterson and Knapp 2018). Quail chicks also consume fire ants, but this reduces quail survival and weight gain (Myers et al. 2014). Numerous species of ectoparasites have been collected from bobwhite quail, but none appear to cause significant impacts on quail population levels (Bergstrand and Klimstra 1964, Doster et al. 1980, Teel et al. 1998, Herzog 2020).

While we could not find studies on fire ant impacts on quail in the LLPE, they have been shown to decrease bobwhite quail chick forage and rest time (Pedersen et al. 1996), and cause significant population declines through mortality (Allen et al. 1993, Giuliano et al. 1996, Mueller et al. 1999, Haines et al. 2017) in other pine forests. However, the magnitude of this impact has been questioned due to the persistence of quail populations in areas with fire ants (Brennan 1993, Brennan et al. 2000). Some land management practices for bobwhite quail—such as disc tilling and prescribed burning intended to increase arthropod biomass (Manley et al. 1994)—may have unintended consequences such as increasing fire ant abundance (Williamson et al. 2002).

Fire ants affect other LLPE vertebrates as well, primarily through predation of egg stages and competition for prey (Allen et al. 1994, 1997). They decrease recruitment in the eastern fence lizard *Sceloporus undulatus* (Bosc & Daudin) (Darracq et al. 2017), reduce herpetofauna abundance and species richness in general (Allen et al. 2017), significantly depredate nestlings of shrub-nesting songbirds (Conner et al. 2010), and have been speculated to contribute to decline in snake populations (Winne et al. 2007, Tuberville et al. 2000). Other relationships are less direct. Southern toads avoid fire ants (Long et al. 2015). Oldfield mice *Peromyscus polionotus* (Wagner) forage less in the presence of fire ants than in their absence (Darracq

et al. 2016) or even the presence of predator urine (Orrock and Danielson 2004).

## Arboreal

We now examine arthropods that depend on longleaf pine trees directly, as well as other tree species of the ecosystem. Research conducted in this stratum includes studies of arboreal ants, prey of the red-cockaded woodpecker, saproxylic insects, and forest pests.

Generally speaking—and with the exception of fire's critical role in maintaining longleaf's dominance of the canopy—fire has a limited role on arboreal arthropods compared to the herbaceous layer.

Prescribed fire results in a higher abundance of buprestids (Sullivan et al. 2003) and species richness of saproxylic insects (Campbell et al. 2008). Some pine phloem-feeding bark beetle species were collected in lower numbers from traps in fire-damaged areas than a control, while the opposite was true for ambrosia beetles (Hanula et al. 2002). Other studies of saproxylic insects demonstrate these species-specific responses as well (Sullivan et al. 2003, Campbell et al. 2008). Some have reported no or little short-term impacts of fire on wood roaches (New and Hanula 1998), arboreal ants (Whitford and Gentry 1981), and red-cockaded woodpecker prey in general (New and Hanula 1998, Taylor 2003).

Prescribed burning affected *Ips* spp. beetle trap catches differently based on site characteristics: in xeric sites fire-excluded areas caught significantly more beetles than frequently burned areas, but in mesic sites fire-excluded areas caught significantly less beetles than frequently burned areas (Ritger 2019). Burn season may also affect arboreal ant and spider biomass (New and Hanula 1998).

This stratum contains numerous arthropods that demonstrate positive pyrotaxy. In the LLPE, Sullivan et al. (2003) observed *Xyleborus pubescens* Zimmerman, *Hylastes salebrosus*, *H. tenuis*, *Pachylobius picivorus*, and jewel beetles (Coleoptera: Buprestidae) exhibiting behavioral attraction to recently burned areas in the weeks following the fire. They suggest that volatile chemicals released by stressed trees in the weeks following the burn are behind this apparent attraction. Frogs possess specialized hearing organs for detecting—and fleeing from—fire (Grafe et al. 2002); this adaptation has been suggested as a possibility in arthropods of the LLPE (Dell et al. 2017) for fire detection in both positively and negatively pyrotaxic species. As smoke can be used as an efficient trapping method for some pyrophilic flies [though not pyrophilic beetles (Milberg et al. 2015)], these species may use it to locate recently burned host material. In Europe, the black fire beetle *Melanophila acuminata* (DeGeer) (Coleoptera: Buprestidae) possesses infrared receptors to detect still-smoldering logs for oviposition, as larvae require freshly fire-killed trees (Evans 1966, Schmitz and Bleckmann 1998). In western North America, the jewel beetle *Xenomelanophila miranda* (LeConte) and *Syntexis libocedrii* Rohwer (Hymenoptera: Anaxyelidae) both have infrared sensors to detect still-smoldering wood as well.

We consider red-cockaded woodpecker prey in this arboreal section, although approximately 40–70% of arthropod biomass on the boles of LLP trees crawl up from the forest floor (Hanula and Franzreb 1998). Important arthropod prey of the red-cockaded woodpecker include roaches (Hanula and Franzreb 1998, Hanula et al. 2000b, Hanula and Engstrom 2001), spiders (Hanula and Franzreb 1998, Hanula and Engstrom 2001), centipedes (Hanula and Engstrom 2001), caterpillars (Hanula and Franzreb 1998, Hanula and Engstrom 2001), woodborer larvae (Hanula and Franzreb 1998), sawfly larvae (Hanula et al. 2000b), and *Crematogaster ashmeadi* Mayr (Hymenoptera: Formicidae) (Hess and James 1998).

Roaches made up as much as 69% of abundance (Hanula and Franzreb 1998) and 55–73% of biomass (Hanula and Engstrom 2001) brought to nestlings by adults. Red-cockaded woodpeckers often forage on dying pines attacked by southern pine beetle and various *Ips* spp., the larvae of which are not generally consumed (Rudolph et al. 2007). The community of this prey may not differ significantly between old-growth and old-field longleaf forests (Hanula and Engstrom 2001), or even between longleaf and loblolly stands (Hanula et al. 2000b). However, longleaf pine trees support a higher abundance and biomass of arthropods on their bark compared to loblolly pine of similar age and size. This is likely due to the more complex bark structure of longleaf pine (Horn and Hanula 2002). A case study in South Carolina, USA showed arthropod biomass to decrease with longleaf tree age on the bole but increase with tree age on both dead and live limbs (Hooper 1996). Total arthropod biomass was found to be the highest for 86-yr-old trees and to decrease with younger or older trees (Hooper 1996, Conner et al. 2004).

For red-cockaded woodpecker diseases and parasites, see Costa and DeLotelle (2007) and Pung et al. (2000a).

*Crematogaster ashmeadi* dominates the arboreal ant community, occurring in ~50% of all longleaf trees sampled (Hahn and Tschinkel 1997, Tschinkel and Hess 1999). Other notable arboreal ant species include *Camponotus nearcticus* Emery, *Leptothorax wheeleri* Smith (Tschinkel 2002), and *Crematogaster pinicola* Deyrup & Cover (Deyrup and Cover 2007). This community, however, changes with the tree age. In young stands, baits attracted ground-nesting ants from the ground, but in larger trees, the community shifts more to arboreal species (Tschinkel and Hess 1999). Larger trees also allow more coexistence of species, with up to 19% of trees having more than one arboreal ant species in the largest sampled pine trees (Tschinkel and Hess 1999).

Arboreal queen ants appear to prefer abandoned beetle galleries in dead branches (Tschinkel and Hess 1999, Tschinkel 2002), and will also inhabit abandoned bark-mining caterpillar *Givira francesca* (Dyar) chambers in the outer-bark of the tree trunk, as well as termite galleries at ground level (Whitford and Gentry 1981, Tschinkel 2002). The distribution of *C. ashmeadi* is affected both by suitable founding sites and interactions with conspecific and heterospecific ant colonies (Hahn and Tschinkel 1997), with tree height and dead branch abundance influencing site selection as well (Baldacci and Tschinkel 1999). Trees likely contain only one colony of *C. ashmeadi* per tree, with the occasional use of multiple trees for a single colony (Tschinkel 2002). *Crematogaster lineolata* (Say) increased in abundance from both natural and experimental warming (Resasco et al. 2014b). Other arboreal ant studies concern distribution and settlement of *C. ashmeadi* (Hahn and Tschinkel 1997, Baladacci and Tschinkel 1999, 2002).

Longleaf pine has long been considered resistant to many insect pests and diseases (Wahlenberg 1946, Snow et al. 1989, Moser et al. 2003, Johnson and Gjerstad 2006), especially those that cause significant problems in other southern pines (such as southern pine beetle, pine tip moth, fusiform rust, annosus root rot, and pitch canker). Still, there are numerous records of insects feeding on longleaf pine, causing various degrees of damage.

The southern pine beetle (SPB) is the most destructive forest pest in the southern United States, readily attacking and killing many species of pine within its range (Price et al. 1992). As far back as 1929 longleaf was noted to be ‘least favored and rarely attacked’ by SPB (St. George and Beal 1929). Modern research has reinforced this observation, if not agreed on the reasons behind it. Martinson et al. (2007) noted that longleaf pine suffers far less mortality from SPB than its sympatric congeners. However, Snow

et al. (1989) cautioned against confusing the species’ resistance to SPB with immunity to attack. Longleaf is subject to successful southern pine beetle attack, but such losses only occur in the midst of explosive SPB outbreaks in nearby loblolly stands (a species viewed as highly susceptible to SPB), or in the face of stresses on host trees (e.g., severe drought) that predispose trees to attack. Still, historically, SPB has been documented to outbreak in longleaf pine forests and kill ‘a great amount of timber’ in eastern Texas, USA between 1882 and 1885 as well as in the early 20th century (Hopkins 1902). Other bark beetles may also affect LLP, especially stressed trees. Black turpentine beetles *D. terebrans*, pales weevil *Hylobius pales* (Herbst), pitch-eating weevil *Pachylobius picivorus*, Carolina pine sawyer *Monochamus carolinensis* (Olivier), southern pine sawyer *M. titillator* (Fabricius), *Hylastes salebrosus*, *Pityoborus* spp. and southern pine engraver beetles *Ips* spp. [*Ips grandicollis* (Eichhoff), *I. avulsus* (Eichhoff), *I. calligraphus* (Germar)] are all frequently captured in the LLPE (Smith 1957, Fatzinger 1985). *Orthotomicus caelatus* (Eichhoff) breeds in thick bark on stumps and logs or at the bases of weakened LLP (Baker 1972). Some degree of natural control of bark beetles is provided by other associated insects such as woodborers, weevils, and termites, which compete with bark beetle larvae for food, predators, and parasitoids (Baker 1972).

Longleaf pine is also relatively resistant to another major forest pest, pine tip moth *Rhyacionia* spp. (Lepidoptera: Tortricidae), which causes significant problems for other pines in the southern United States (Asaro et al. 2003). This near immunity to tip moth may reflect the evolutionary advantages of having only one terminal bud in the grass stage (Snow et al. 1989). In contrast, longleaf pine cones and shoots appear especially susceptible to insect pests in general (McLemore 1977, White et al. 1977), including *Ernobius granulatus* LeConte (Coleoptera: Ptinidae) (Allen and Coyne 1956), and the pitch moth *Dioryctria* spp. (Lepidoptera: Pyralidae) (Allen and Coyne 1956, McLemore 1977, Meeker 2004). *Cydia ingens* (Heinrich) (Lepidoptera: Tortricidae) may also cause serious losses in seed orchards, although it does not in natural regeneration (Coyne 1968). Likewise, seed predators may cause as much as 99% LLP seed mortality in some cases (Boyer 1964). In addition, spider mites and aphids (Hemiptera: Aphidae: *Cinara* spp.) feed on foliage, jewel bugs (Hemiptera: Scutelleridae) feed on cones, stink bugs (Hemiptera: Pentatomidae) feed through the bark, scarab beetles *Phyllophaga luctuosa* (Horn) feed on roots, the jewel beetle *Chrysobothris* sp., as well as the turpentine borer *Buprestis apricans* Herbst, bore and feed in the mainstem of LLP (Baker 1972). In fact, the turpentine borer was once the most destructive insect in the turpentine orchards of the southern United States (Baker 1972). Longleaf pine is also listed as a host for native siricid woodwasps, *Sirex edwardsii* Brulle and *S. nigricornis* Fabricius (Smith and Schiff 2002). Of more recent, exotic invasive, pestiferous insects, LLP shows susceptibility to the European woodwasp *Sirex noctilio* Fabricius (Dinkins 2011, Bookwalter et al. 2019) but seems to be virtually immune to the pine shoot beetle *Tomicus piniperda* (L.) (Eager et al. 2004). Fire ants can destroy germinating longleaf seeds, but not established seedlings (Campbell 1974).

Although other species may not be documented due to a concentration on economically significant pests, Folkerts et al. (1993) list only 42 arthropods known to attack unweakened LLP. Sawflies *Xyela minor* Norton and *X. bakeri* Konow occur and develop on longleaf (Ebel 1966) but apparently do not reach problematic levels.

A recently felled longleaf pine produced 53 species of insects—including over 300 beetle specimens—in just 2 h of collecting efforts (Davis and Leng 1912). Arthropod use of logs did not increase with burn frequency, despite less leaf litter and shrub cover (Hanula et al. 2009).

## Conclusions and Future Research Priorities

As efforts increase to restore longleaf pine to more of the landscape it once dominated, it will be beneficial to likewise increase our efforts to understand the identity and roles of the organisms that call it home, and the roles that frequent fire plays in restoring and maintaining the almost overwhelming diversity of species, guilds, and ecological services present in this vanishing ecosystem. Efforts must focus on determining the species essential to the success of a diverse LLPE. Pollinators may be especially important and have received some focus. Rare and threatened species may serve as foci for restoration of specific habitats (and thereby of associated species and ecological community attributes). Arthropods may act as indicator species as well, with changes in number and distribution signifying both beneficial and deleterious changes in ecosystems. Typically ground beetles, bees, and ants are chosen as indicator species; others may exist within the diversity of LLPE community and habitat types. However, research on ground beetles in the LLPE is lacking, represented by only a few studies (Harris and Whitcomb 1971, 1974), though this taxon is seen as a reliable indicator of disturbance in other systems (Rainio and Niemälä 2003, Pearce and Venier 2006). Particular species of ants *T. septentrionalis* (Seal and Tschinkel 2006), springtails *Sminthurus* spp. (Collembola: Sminthuridae), planthoppers *Metcalfa pruinosa* (Say) (Hemiptera: Flatidae), leafhoppers *Erythroneura* sp., *Empoasca* sp. and *Jikradia olitoria* (Say) (Hemiptera: Cicadellidae), and jumping spiders *Hentzia palmarum* (Hentz) (Araneae: Salticidae) may also be useful as specific indicators (Provencher et al. 2000).

Indicator taxa may also play a role in the ongoing study and debate over global arthropod declines. While some authors warn of exaggerated media coverage and mistrust in science (Saunders et al. 2019) or emphasize that there is not enough information to conclude that all insects are declining in all locations (Eggleton 2020), the need for more specific research is indisputable. This is especially true considering that the most recent estimate suggests only 20% of terrestrial arthropod species in the world have been described (Stork 2018). To that end, we have initiated a long-term study of arthropod presence and abundance at the Jones Center at Ichauway. In our Trends in Arthropod Biodiversity Systems study, initiated in 2020, we are measuring arthropod abundance and diversity in four ecological communities (fallow agricultural fields, flatwoods, fluvial terraces, and uplands) using multiple trapping methods to begin to establish a lasting database for monitoring arthropods in this amazing longleaf pine forest. Our hope is to export this model to other ecosystems and develop standard approaches, datasets, and measures to contribute to our understanding of insect numbers on a wide scale.

Regardless of overall approaches or particular areas of emphasis, the LLPE has the potential to serve as a model system for studies of complex interactions among the most diverse assemblages of species to be found anywhere in the temperate zone. Arthropods, relatively understudied in longleaf if only due to their speciose nature in general, are an especially critical piece of the puzzle. We hope that the solid base of information we have summarized here provides inspiration and a jumping off point for further investigations, insights, and action.

## Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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