Arthropod Abundance and Biomass in Response to *Pinus taeda* L. Trunk Height¹

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Abstract The trunks of southeastern pines provide vital habitat for many invertebrates that are, in turn, available as prey for bark-foraging birds. Knowing how these arthropods are distributed vertically on tree trunks is important and may allow for a rapid assessment of prey response to forest management practices. In this study, we used a fast-acting insecticide to sample the arthropods on the lower (0-3 m) and upper (3-9 m) bole sections of nine loblolly pine, Pinus taeda L., trees. We collected over 1,600 arthropods representing 15 orders and 66 families. Ants (Hymenoptera: Formicidae) were the most abundant group collected, and wood cockroaches (Blattodea: Blattellidae) accounted for the greatest overall biomass. Abundance and biomass of arthropods per m² were greater on the lower trunk, but these values were strongly correlated with those from the upper trunk. Nonmetric multidimensional scaling and permutational multivariate analysis of variance showed that arthropod community composition differed significantly between the two trunk positions. Additionally, indicator species analysis found four flightless taxa to be significantly associated with the lower trunk (Araneae, Zygentoma, Hymenoptera, and Pseudoscorpiones) but none with the higher trunk position. These findings show that bark-dwelling arthropods are generally more abundant near the bases of trees and that there is a strong relationship between abundance and biomass between lower and upper trunk sections. Knockdown insecticides offer an effective tool for rapidly assessing the availability of invertebrate prey for bark-foraging birds.

Key Words biomass, tree trunk, arthropods, bark-foraging, red-cockaded woodpecker

Tree trunks or boles and associated bark habitats provide important resources for many invertebrates and a productive foraging substrate for many of their avian predators. It was initially thought that tree trunks only supported a small community of relatively immobile arthropods or that they serve simply as spots for egg laying or overwintering. However, Moeed and Meads (1983) studied arthropod use of four tree species in New Zealand and found that tree trunks are important for linking the forest floor to the canopy. Likewise, Hanula and Franzreb (1998) sampled arthropods on longleaf pine (*Pinus palustris* Miller) and demonstrated that few of the species they captured lived exclusively on the bark; rather, they came in from other habitats (i.e., woody debris, detritus, soil layer, or vegetation). Tree trunks not only serve as travel corridors but also are a vital habitat component for many arthropods seeking to find food, mates, or shelter (Majer et al. 2003, Wade and

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Leather 2002) and no doubt play a part in sustaining invertebrate biodiversity (Pinzón and Spence 2010 and sources therein). Many factors contribute to the abundance, diversity, and distribution of arthropods on tree trunks, but none seem as important as bark structure. For example, Nicolai (1986) found that European trees with fissured bark supported a more diverse arthropod fauna than smooth-barked trees and attributed this to the complexity of microstructures and microclimates found there. Mariani and Manuwal (1990) also noted greater spider abundance on trees with more deeply fissured bark. Likewise, Hanula et al. (2000a) found a positive correlation between abundance and biomass of arthropods and longleaf pine bark thickness, and Horn and Hanula (2002a) demonstrated that the flaky, overlapping nature of longleaf pine bark supported greater numbers and biomass than did loblolly pine (*Pinus taeda* L.).

The above studies provide clear evidence that many flightless arthropods inhabiting tree trunks only use the habitat part-time, with a majority of the species being generalists that climb up the tree from the soil and litter layer. There are, however, many unique situations that exist that create either obligatory associations or demonstrate strong preferences for tree species or bark textures. For example, André (1985) found some arthropods were confined to the microenvironments created by epiphytic lichen and algae cover on bark. Proctor et al. (2002) reported that oribatid mites captured on hoop pine (Araucaria cunninghamii Mudie) represented resident populations that seemed to use the trunk as a full-time habitat rather than a travel corridor. Similar results were found by Lindo and Winchester (2007) on western red cedar (Thuja plicata Donn ex D. Don) where oribatid mite communities varied depending on vertical distance from the ground. Additional studies have shown that spiders, predators whose diversity is linked to habitat complexity (Larrivee and Buddle 2010), often show preference to specific tree species (Blick 2011, Curtis and Morton 1974). Because trunk arthropods are abundant, diverse, and easy to collect, they serve as model organisms for studying various aspects of ecology, that is, shifts in local climatic conditions (Prinzing 2005), urban encroachment (Su et al. 2010), or forest cover type (Pinzón and Spence 2010). However, they can also be used as a focal group to determine how forest conditions or management practices affect prey availability for bark-gleaning birds.

Mariani and Manuwal (1990) reported that brown creeper (Certhia americana Bonaparte) abundance on Douglas fir (Pseudotsuga menziesii Mirbel Franco) was correlated with the abundance of spiders inhabiting the bark, and Halaj et al. (2009) found that green-tree retention treatments had mostly positive effects on barkdwelling arthropod abundance available to brown creepers. Similar work conducted in the southeastern United States examined bark-dwelling arthropods occurring on pines, particularly those located in foraging areas of the red-cockaded woodpecker (Leuconotopicus borealis Vieillot). Several studies have examined commonly selected prey fed to red-cockaded woodpecker nestlings (Hanula and Franzreb 1995, Hanula and Engstrom 2000, Hanula et al. 2000b, Hess and James 1998). These studies showed that, although many arthropod taxa were readily consumed, a common few composed the bulk of the red-cockaded woodpecker diet (i.e., wood roaches, spiders, and ants) and that these prey also occur in alternative habitats (Hanula and Franzreb 1998, Horn and Hanula 2002b, Horn and Hanula 2008). Studies have shown that some arthropod communities vary with the vertical profile of the tree (Lindo and Winchester 2007); however, limited evidence exists for arthropod biomass stratification on southern pines as it relates to bark-foraging birds. Of the known studies that have evaluated the vertical distribution of prey available on southern pines (Collins et al. 2002, Hanula and Franzreb 1998, Hooper 1996), no definitive conclusion has been reached; however, in general, the lower bole appears to support greater numbers and biomass of arthropods.

In the southern United States, the loblolly-shortleaf pine forest type comprises 14% of total land cover and, yet, accounts for 71% of softwood volume (Oswalt et al. 2014). Likewise, numerous bark-gleaning birds are known to utilize the bole of loblolly pine to find prey (Hamel 1992), demonstrating its importance to the overall food web. To evaluate responses of bark arthropods to loblolly pine management, it is imperative to develop monitoring programs that accurately reflect their abundance at the time of sampling. To date, several methods have been used to assess arthropod abundance on southern pine tree trunks, with the most common being bark scraping (Hanula and Franzreb 1998, Hooper 1996), burlap bands (Horn and Hanula 2008), crawl traps (Hanula and New 1996, Horn and Hanula 2008), sticky traps (Collins et al. 2002), and insecticide treatments (Horn and Hanula 2002a). Of these methods, only burlap bands, bark scraping, and insecticide application provide a "standing crop" (present at the time of sampling) estimate of arthropod abundance and biomass. Because previous work showed it to be a useful technique for rapidly sampling arthropods on tree trunks (Horn and Hanula 2002a), our objective was to use knockdown insecticides to determine if there was a relationship between arthropod biomass and abundance on both the upper and lower boles of loblolly pine and how the arthropod community might differ at the two positions.

Materials and Methods

Study site. We conducted this study at the Savannah River Site (SRS), an 80,270-ha United States Department of Energy nuclear production facility located in the upper Atlantic Coastal Plain Physiographic Province. Before European arrival, longleaf pine dominated the dry sandhill habitats at SRS, whereas loblolly pine was more prevalent in low-lying riparian forests. Upland locations on the SRS currently contain artificially regenerated loblolly, slash (Pinus elliottii Engelmann), and longleaf pine stands that were established on abandoned agricultural land (Knox and Sharitz 1990). These managed, old-field pine plantations now comprise approximately 53,014 ha (68%) of the forest cover, with loblolly pine being the dominant species present. Management of red-cockaded woodpeckers at SRS occurs predominantly in these upland pine forests, which contain most of the suitable habitat and are within the designated primary habitat management area for the woodpecker (Johnston 2005). Management within these areas is typical of that for the red-cockaded woodpecker and include midstory control measures (prescribed fire, mechanical removal, and herbicides) and long rotations (100 y for loblolly and 120 y for longleaf). Understory vegetation species within these stands are highly varied but typically include broom sedge (Andropogon virginicus L.), bracken fern (Pteridium aquilinum [L.] Kuhn), poison oak (Toxicodendron pubescens Miller), deerberry (Vaccinium stamineum L.), sparkleberry (Vaccinium arboreum Marshall), wax myrtle (*Myrica cerifera* [L.] Small), sweetgum (*Liquidam-bar styraciflua* L.), and scrub oaks (*Quercus* spp.) (Imm and McLeod 2005).

Hanula and Franzreb (1998) sampled arthropods on longleaf pine trees and demonstrated that many only use tree trunks as a part-time habitat. One alternate habitat feature that has been shown to be important to many of these bark-inhabiting arthropod taxa is coarse woody debris (Horn and Hanula 2008). Previous work from the same area utilized in this study showed that average dead wood volumes were 2.14 m³/ha for standing dead trees and 6.45 m³/ha for logs on the ground within these upland pine stands (Horn and Hanula 2002b).

Arthropod sampling. In April 2005, we selected nine loblolly pine trees (45-50 y old based on stand establishment data) that averaged 39.80 cm in diameter at breast height for arthropod sampling. Our objective was to determine if arthropod biomass, abundance, and composition varied between the easily accessible lower portion of the trunk and the upper tree trunk. We sampled arthropods using Pounce 5.2 EC (FMC, Philadelphia, PA), a synthetic pyrethroid insecticide (1% AI) that quickly immobilizes most arthropods, applied from a hydraulic lift truck to two sections of bole (0-3.05 m and 3.05-9.29 m) (Fig. 1A) over 2 days. The height of the lower section was chosen because that portion of the tree trunk could easily be spraved from the ground without the lift truck. Upper sections represented the "remaining bole" up to the first live branch and were sprayed from the lift truck (Fig. 1B). Lower sections were collected on the first day and higher sections the second day because the solution would run down the tree bole (i.e., to avoid contamination). Despite working rapidly on arthropods, pyrethroids have been shown to be nontoxic to birds and there appear to be no adverse effects on avian wildlife following sublethal exposures (Gupta 2012). A 7.6-L handheld sprayer with a wand was used to ensure that the mixture could be directly applied to the tree bole only. The solution was applied as a fine mist and sprayed until the bole was saturated to the point of runoff. Arthropods that fell were collected on 2 tarps (3 \times 3.5 m) placed at the base of trees (Fig. 1C) over a period of 1 h and then immediately placed into 70% ethanol for later identification.

Statistical analyses. All arthropods were identified to the lowest taxonomic level possible by using a reference collection housed at the USDA Forest Service, Southern Forestry Sciences Laboratory in Athens, GA. Arthropods were then ovendried at 40°C for 48 h and weighed to obtain biomass estimates. We used a paired *t*-test (SAS 2000) to test for differences in arthropod abundance and biomass between the upper and lower sections of tree trunk. Because the surface area sampled varied from tree to tree and between sections of trunk, we standardized abundance and biomass by surface area (total abundance or biomass/m²) by using the total length of each section sprayed and the midpoint diameter to calculate surface area sampled. Simple linear regression analyses (PROC GLM, SAS 2000) were used to examine the relationship of arthropod abundance and biomass on the lower trunk with that on the upper trunk.

We used the PC-ORD package (McCune and Mefford 2011) to perform nonmetric multidimensional scaling, using the Bray-Curtis distance measure, to assess differences in invertebrate community composition between heights. The dataset was limited to orders present in at least 3 of the 18 samples, resulting in a matrix with 12 invertebrate orders. We used data standardized by bark surface area and relativized by species (i.e., order) maximum prior to analysis. We also used PC-

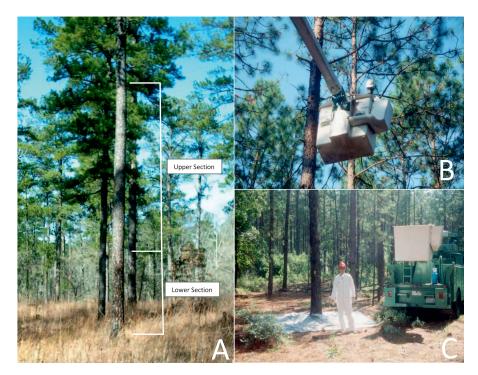


Fig. 1. A) Loblolly pine showing upper and lower trunk sections that were treated with insecticide so that collections of arthropods could be made. B) Bucket truck access to portions of the canopy allowed for sampling greater bole heights. C) Tarps placed at the base of the tree assisted in collections of arthropods.

ORD to perform one-way permutational multivariate analysis of variance (to determine whether assemblages were significantly different between the two positions) as well as indicator species analysis by using the same dataset. Following the approach of Dufrêne and Legendre (1997), indicator species analysis was used to assess order-level associations with respect to trunk position.

Results

A total of 1,618 arthropods representing 66 families in 15 orders were collected (Table 1). Hymenoptera (99% were ants) accounted for the greatest abundance (n = 498), followed by Zygentoma (silverfish) (n = 270), Blattodea (wood cockroaches) (n = 255), Araneae (spiders) (n = 218), and Coleoptera (beetles) (n = 206). Wood cockroaches accounted for 43% of the total biomass collected from tree trunks. Beetles made up the second highest biomass total (20%), followed by Hemiptera (true bugs) (18%), silverfish (9%), and spiders (7%). Beetles were the most diverse order (40 genera), followed by spiders (21 genera), ants and wasps (9 genera), and true bugs (7 genera).

^r able 1. Total number and biomass (g/m ²) for arthropods collected from the upper and lower trunk of loblolly pine trees a the Savannah River Site (Aiken County, SC) using a knockdown insecticide.

$n/m^2 \pm SE$ $g/m^2 \pm SE$ 3.5 ± 0.33 0.009 ± 0.002 2.5 ± 0.51 0.059 ± 0.017 0.14 ± 0.08 0.0005 ± 0.003 2.3 ± 0.67 0.022 ± 0.004 0.3 ± 0.1 0.0001 ± 0.0001 0.3 ± 0.14 0.0001 ± 0.0001 0.3 ± 0.14 0.026 ± 0.007 0.3 ± 0.14 0.026 ± 0.007 0.65 ± 0.044 0.0001 ± 0.00014 0.05 ± 0.044 0.0001 ± 0.00014 0.03 ± 0.03 0.0001 ± 0.00014 0.03 ± 0.03 0.0001 ± 0.00014 (ers) 0.1 \pm 0.060 0.0001 ± 0.00014 0.1 \pm 0.066 0.0001 ± 0.00014 0.00012 ± 0.00013 4.1 \pm 0.7 0.0015 ± 0.00032 0.00011 ± 0.00002		Lov	Lower Trunk	Upp	Upper Trunk
3.5 ± 0.33 0.009 ± 0.002 $1.15 \pm$ 2.5 ± 0.51 0.059 ± 0.017 $1.97 \pm$ 2.5 ± 0.51 0.005 ± 0.0003 $0.18 \pm$ 0.14 ± 0.08 0.0005 ± 0.0004 $1.4 \pm$ 0.3 ± 0.1 0.0001 ± 0.0001 $0.12 \pm$ 0.3 ± 0.14 0.0026 ± 0.007 $0.12 \pm$ 0.5 ± 0.04 0.0001 ± 0.0001 $0.03 \pm$ 0.05 ± 0.04 0.0001 ± 0.00004 $0.012 \pm$ 0.03 ± 0.03 0.0001 ± 0.00004 $0.012 \pm$ 0.03 ± 0.03 0.0001 ± 0.0001 $0.012 \pm$ 0.03 ± 0.03 0.0 ± 0.00 0.01 ± 0.0001 0.0001 ± 0.000 0.00 ± 0.00 $0.01 \pm$ 0.1 ± 0.000 0.0001 ± 0.00002 $0.016 \pm$ 0.015 ± 0.0003 $0.016 \pm$ $0.001 \pm$	Order		11	+1	$g/m^2 \pm SE$
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Araneae (spiders)	3.5 ± 0.33	0.009 ± 0.002	1.15 ± 0.17	0.006 ± 0.001
) 0.14 ± 0.08 0.0005 ± 0.0003 0.18 ± 0.1 2.3 ± 0.67 0.022 ± 0.004 $1.4 \pm 1.4 \pm 0.001$ 0.3 ± 0.1 0.0001 ± 0.0001 $0.12 \pm 0.03 \pm 0.031 \pm 0.0003$ 0.6 ± 0.14 0.026 ± 0.007 $0.31 \pm 0.12 \pm 0.033 \pm 0.033 \pm 0.033 \pm 0.033 \pm 0.0001 \pm 0.00004$ 0.05 ± 0.04 0.0001 ± 0.00004 $0.03 \pm 0.03 \pm 0.033 \pm 0.033 \pm 0.033 \pm 0.0033 \pm 0.0001 \pm 0.00004$ $0.012 \pm 0.033 \pm 0.033 \pm 0.033 \pm 0.033 \pm 0.001 \pm 0.00001 \pm 0.00001 \pm 0.0001 \pm 0.00002 \pm 0.00002 \pm 0.00002 \pm 0.0001 \pm 0.00002 \pm 0.0001 \pm 0.00002 \pm 0.0001 \pm 0.00002 \pm 0.00002 \pm 0.0001 \pm 0.00002 \pm 0.0002 \pm 0.00002 \pm 0.0002 \pm 0.0002$	Blattodea (roaches)	2.5 ± 0.51	0.059 ± 0.017	1.97 ± 0.39	0.032 ± 0.009
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Chilopoda (centipedes)	0.14 ± 0.08	0.0005 ± 0.0003	0.18 ± 0.05	0.002 ± 0.001
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Coleoptera (beetles)	2.3 ± 0.67	0.022 ± 0.004	1.4 ± 0.51	0.018 ± 0.0069
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Diptera (flies)	0.3 ± 0.1	0.0001 ± 0.0001	0.12 ± 0.04	$0.0001 \pm .00002$
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Hemiptera (true bugs)	0.6 ± 0.14	0.026 ± 0.007	0.31 ± 0.06	0.013 ± 0.003
9.3 ± 2.56 0.006 ± 0.003 $2.1 \pm$ 0.09 ± 0.04 0.0001 ± 0.00004 $0.12 \pm$ 0.03 ± 0.03 0.001 ± 0.0001 $0.01 \pm$ 0 ± 0 0.0 ± 0.0 $0.01 \pm$ 0 ± 0 0.0 ± 0.0 $0.01 \pm$ 0 ± 0 0.0 ± 0.0 $0.01 \pm$ $0.12 \pm 0.002 \pm 0.001$ 0.01 ± 0.001 $0.01 \pm$ 0.1 ± 0.06 0.002 ± 0.001 $0.01 \pm$ 0.6 ± 0.09 0.0001 ± 0.00002 $0.16 \pm$ 4.1 ± 0.7 0.015 ± 0.003 $0.16 \pm$	Hemiptera (hoppers)	0.05 ± 0.04	0.0001 ± 0.00004	0.03 ± 0.02	$0.0001 \pm .00005$
0.09 ± 0.04 0.0001 ± 0.00004 0.12 ± 0.012 ails) 0.03 ± 0.03 0.03 ± 0.03 0.001 ± 0.0001) 0 ± 0 0.0 ± 0.0 0.01 ± 0.001) 0 ± 0 0.0 ± 0.0 0.02 ± 0.0 legs) 0 ± 0 0.0 ± 0.0 0.01 ± 0.001 0.11 ± 0.06 0.0002 ± 0.0001 0.015 ± 0.003 4.1 ± 0.7 0.015 ± 0.003 0.16 ± 0.06	Hymenoptera (ants)	+1	0.006 ± 0.003	+1	0.002 ± 0.001
ails) 0.03 ± 0.03 0.001 ± 0.0001) 0 ± 0 0.0 ± 0.00 legs) 0 ± 0 0.0 ± 0.0 lers) 0.1 ± 0.06 0.0002 ± 0.0001 0.6 ± 0.09 0.0001 ± 0.0002 4.1 ± 0.7 0.015 ± 0.003	Lepidoptera (moths)	0.09 ± 0.04	0.0001 ± 0.00004	$0.12\ \pm\ 0.05$	0.0004 ± 0.0002
0 ± 0 0.0 ± 0.0 legs 0 ± 0 0.0 ± 0.0 0.1 ± 0.06 0.0002 ± 0.0001 0.6 ± 0.09 0.0001 ± 0.00002 4.1 ± 0.7 0.015 ± 0.003	Microcoryphia (bristletails)	0.03 ± 0.03	0.0001 ± 0.0001	0.01 ± 0.01	*
legs) 0 ± 0 0.0 ± 0.0 ers) 0.1 ± 0.06 0.0002 ± 0.0001 0.6 ± 0.09 0.0001 ± 0.00002 4.1 ± 0.7 0.015 ± 0.003	Neuroptera (lacewings)	0 + 0	0.0 ± 0.0	0.02 ± 0.01	*
$\begin{array}{cccccccc} \text{iers}) & 0.1 \pm 0.06 & 0.0002 \pm 0.0001 \\ 0.6 \pm 0.09 & 0.0001 \pm 0.00002 \\ 4.1 \pm 0.7 & 0.015 \pm 0.003 \end{array}$	Opiliones (daddy long legs)	0 + 0	0.0 ± 0.0	0.01 ± 0.01	*
$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	Orthoptera (grasshoppers)	0.1 ± 0.06	0.0002 ± 0.0001	0.05 ± 0.02	0.0002 ± 0.0001
4.1 ± 0.7 0.015 ± 0.003	Pseudoscorpiones	0.6 ± 0.09	0.0001 ± 0.00002	0.16 ± 0.08	*
	Zygentoma (silverfish)	4.1 ± 0.7	0.015 ± 0.003	$1.53\ \pm\ 0.23$	0.006 ± 0.0013

* Denote negligible weights.

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We collected significantly more arthropods (n/m^2) on the lower bole $(23.71 \pm 3.79 [\bar{x} + SE])$ than on the upper bole $(9.16 \pm 1.62) (t=5; df=8; P=0.0011)$ and more arthropod biomass (g/m^2) on the lower bole (0.14 ± 0.03) than on the upper bole $(0.08 \pm 0.02) (t=2.97; df=8; P=0.0178)$. Arthropod abundance on lower sections of the tree was 2.6 times greater than the upper trunk and the biomass was 1.8 times greater. Common arthropod taxa differed between the two trunk regions as well (Table 1). For example, ants (t=3.17; df=8; P=0.0131), spiders (t=5.37; df=8; P=0.0007), and beetles (t=2.67; df=8; P=0.0282) exhibited significantly greater abundance on lower bole sections, and the same was true for wood cockroach biomass (t=2.88; df=8; P=0.0207). Silverfish are also common residents of pine tree boles that were found in significantly greater numbers (t=4.12; df=8; P=0.0034) and biomass (t=2.89; df=8; P=0.0202) on lower sections of the tree.

Overall abundance (y = 2.15 + 0.29x, r² = 0.48, P < 0.04) and biomass (y = 0.02 + 0.46x, r² = 0.49, P < 0.04) on the lower trunk were correlated with those values from the upper trunk (Fig. 2A, B). We were particularly interested in wood cockroach biomass because previous studies have shown their importance as prey items fed to red-cockaded woodpecker (Hanula and Franzreb 1995, Hanula and Engstrom 2000, Hanula et al. 2000b) and red-bellied woodpecker (*Melanerpes carolinus* L.) (Jackson 1976) nestlings, and due to their abundance, it is likely that they are important to other avian predators as well. Our findings demonstrate a strong correlation between wood cockroach biomass (y = 0.0036 + 0.4949x, r² = 0.84, P < 0.0005) on lower and upper pine boles showing that weights closer to the ground are reflective of available prey biomass higher up the tree (Fig. 3).

Nonmetric multidimensional scaling yielded a two-dimensional solution with a final stress of 15.08. It is clear from the ordination that invertebrates sampled from lower and upper bole positions formed distinct groups and, based on permutational multivariate analysis of variance, community composition differed significantly between the two positions (F1,16 = 6.2, P < 0.001) (Fig. 4). Indicator species analysis found four taxa to be significantly associated with the lower bole position: Araneae (IV = 75, P = 0.0002), Zygentoma (IV = 73, P = 0.003), Pseudoscorpiones (IV = 70.4, P = 0.008), and Hymenoptera (IV = 81.7, P = 0.011). No taxon was significantly associated with the upper trunk position.

Discussion

Previous research has revealed that a diverse arthropod community resides on and underneath the bark of trees (Adis 1988, Majer et al. 2003, Moeed and Meads 1983, Peck et al. 2014, Pinzón and Spence 2010). In this study, we collected over 1,600 arthropods from 66 families, and our findings were consistent with previous reports from the southeastern United States that showed that, despite a wide range of taxonomic groups contributing to the bark fauna of pines, there are a predictable few that are the most abundant and comprise most of the biomass. For example, Hooper (1996) investigated dormant season arthropod biomass by examining bark scrapings from longleaf pine. When only the trunk was considered (as in this study), he found the greatest biomass consisted of, in decreasing order, true bugs, spiders, and wood roaches. Likewise, other studies utilized passive crawl traps capturing

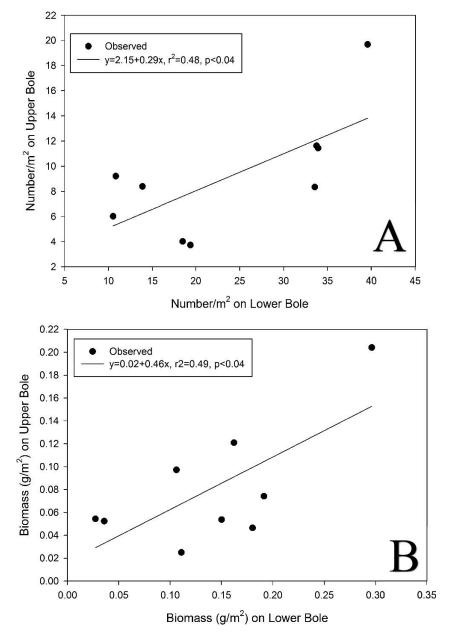


Fig. 2. A) Simple linear regression showing relationship of number of arthropods collected (per m²) on the upper and lower bole of loblolly pine. B) Simple linear regression showing relationship of arthropod biomass (per m²) on the upper and lower bole of loblolly pine.

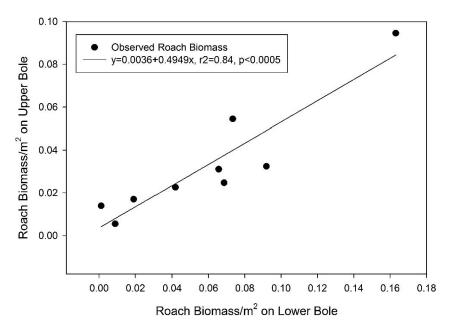


Fig. 3. Simple linear regression showing correlation of wood cockroach biomass on lower and upper sections of loblolly pine tree boles.

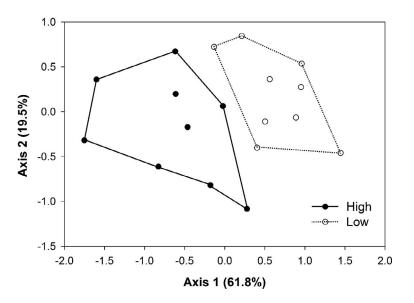


Fig. 4. Ordination from nonmetric multidimensional scaling showing differences in invertebrate assemblages between high (solid dots and lines) and low bole (open dots and dashed lines) positions.

arthropods actively moving up and down the trunk, on both longleaf (Hanula and Franzreb 1998, Hanula et al. 2000a) and loblolly (Horn and Hanula 2008) pine. Despite focusing on different pine species, the collections from these studies were remarkably similar and dominated by ants, spiders, beetles, true bugs, and wood roaches. Horn and Hanula (2002a) directly compared arthropod communities residing on the trunks of both longleaf and loblolly pine and found that even though longleaf pine harbored greater abundance and biomass of arthropods, the community composition residing on the two trees was similar.

In the present study, ants were collected in greater numbers than any other taxonomic group, consistent with other surveys of corticolous arthropod communities that found them to be among the most common groups on tree trunks (Hanula and New 1996, Hanula et al. 2000a, Horn and Hanula 2008, Ramsey 1941). This is also not surprising given that ants are often ecologically dominant within an area where they can comprise a substantial portion of the total biomass (Wilson and Hölldobler 2005). The ants collected most frequently belonged to the genera Crematogaster (acrobat ants) and Camponotus (carpenter ants), both of which are common pine bole residents (Hahn and Tschinkel 1997, Hanula and Franzreb 1995. Hanula and Franzreb 1998. Hess and James 1998. Tschinkel 2002). Carpenter ants can be found nesting in both living and dead trees (Hansen and Klotz 2005) and contribute to ecosystem function by aiding in the decomposition processes, as well as serving as prey to birds (Beal 1911, Cruz and Johnston 1979, Hanula and Franzreb 1995, Sanders 1964, Torgersen and Bull 1995) and even bears (Swenson et al. 1999). Crematogaster spp. are also important to the food web where foraging birds take advantage of their presence on trees (Hanula and Franzreb 1995, Hess and James 1998, Vishnudas 2008). Crematogaster ants seem especially prevalent in pine forests, comprising as much as 80% to 90% of individuals on trees (Tschinkel and Hess 1999). These ants are no doubt important to pine ecosystems given that colonies can number into the tens of thousands (Tschinkel and Hess 1999), which appears to be a plausible explanation as to why they were numerically dominant in this study.

Two other groups of arthropods found in substantial densities on tree boles during our study were silverfish (Zygentoma) and spiders (Araneae). Silverfish (in this case, Thermobia spp.) are common, yet overlooked, flightless residents of southern pines and little is known of their natural history. Due to their presence under the bark of pines, however, they serve as prey to foraging red-cockaded woodpeckers (Hanula et al. 2000b), and because many insectivorous birds are generalists (Gunnarsson 2007) that select prey relative to availability (Hanula and Horn 2004), they are likely important to other species as well. Spiders (Philodromidae, Lycosidae, and Salticidae) were the third most abundant arthropod group captured here and have been routinely listed as common inhabitants of bark microhabitats (Blick 2011, Horton et al. 2001, Horvath et al. 2005, Koponen 1996, Machač and Tuf 2016, Simon 1991), with some living exclusively on tree trunks (Pinzón and Spence 2010). Likewise, they are a well-known prey group for many bark foragers (Hanula and Franzreb 1995, Hanula and Engstrom 2000, Hanula et al. 2000b, Hogstad 1984, Jäntti et al. 2001, Mariani and Manuwal 1990, Morse 1967, Peterson et al. 1989, Williams and Batzli 1979), and based on a review of the literature, bird predation can significantly deplete spider populations (Gunnarsson 2007), so it is likely that spiders are important to the life history of many birds.

Abundance is one way to measure how relevant a particular group is to community function, but biomass is perhaps more important, given that insects account for 90% of secondary production in ecosystems (Price 1984); therefore, it is commonly used as a measure of food availability by avian biologists (Duguay et al. 2000 and sources therein). Our knockdown insecticide treatments indicated that arthropod biomass on loblolly pine trunks was dominated by wood roaches, followed by beetles and true bugs. Wood roaches in the genus Parcoblatta are common and ubiquitous inhabitants of tree trunks but can be found in many other habitats within pine forests (Horn and Hanula 2002b). Due to the fact that they are numerically abundant, found in various local environments, and constitute a significant amount of biomass, wood roaches are very likely important prey for birds that spend time foraging on pines. In fact, wood roaches account for a substantial proportion of prey fed to nestlings of both red-bellied (Jackson 1976) and redcockaded woodpeckers (Hanula and Franzreb 1995, Hanula and Engstrom 2000, Hanula et al. 2000a). Knowing how these common arthropods are distributed vertically on trees could lead to more confident predictions about how management affects their availability to bark-foraging birds.

After standardizing by bark surface area, we found the total arthropod abundance on the lower trunk to be more than twice that on the upper section of tree, and the biomass collected from the same area was 1.75 times greater, which is similar to the findings of Hanula and Franzreb (1998). Although their passive sampling methods (crawl traps and flight traps) yielded similar arthropod densities vertically along the bole, bark scraping, a technique that captures potential prev in "real time" documented significantly greater densities lower on the trunk. Bark scraping also resulted in more biomass at the base of the trunk, although the relationship was not significant. Interestingly, they found wood roach size declined with tree height, a finding repeated in this study. Hooper (1996) used bark scraping at different heights and found both wood roach and ant weights to be greater on lower tree sections. Additionally, a study that focused on Crematogaster ants found the density of chambers and ants were highest in the base and dropped dramatically the higher up the tree (Tschinkel 2002). Thus, it is not surprising that some birds have been observed to focus their foraging efforts on lower sections of trees (Airola and Barrett 1985, Flemming et al. 1999, Franzreb 1985, Weikel and Hayes 1999), likely taking advantage of this increased concentration of prey.

One area that has received less attention is how arthropod community composition varies vertically along the tree bole, although Lindo and Winchester (2007) suggest certain groups stratify themselves on tree trunks based on environmental conditions. Ordination from nonmetric multidimensional scaling revealed differences in invertebrate assemblages between the two trunk sections in this study (Fig. 4), suggesting certain taxa may prefer different locations on the tree trunk. Spiders, silverfish, pseudoscorpions, and ants (nonalate) were all indicator species significantly associated with lower portions of the tree trunk. This is not surprising given that each of these taxa is flightless and a majority of arthropods occurring on tree boles are transients that use it as a part of their habitat, with most crawling up from the ground and litter layer (Hanula and Franzreb 1998, Horn and Hanula 2008, Moeed and Meads 1983, Nicolai 1986). Thicker, more creviced or overlapping bark at the base of many trees harbors many invertebrates (Horn and Hanula 2002a, Nicolai 1986) and may explain why we collected larger

wood roaches there. Studies suggest birds adjust their foraging behavior to these areas during short-term inclement weather events (Dolby and Grubb 1999, Grubb 1975, Grubb 1977), possibly because more prey harbor there at such times.

More than half of the bird species in the United States are insectivorous, and 96% of North American terrestrial birds utilize arthropods as prey for their young (Messick et al. 2018). Studies have shown that insectivores are especially vulnerable to various environmental changes (Castelletta et al. 2000, Hallmann et al. 2017, Sodhi 2002), which is not surprising given that invertebrate biomass has been positively correlated to bird abundance (Holmes et al. 1986). Many birds acquire a large portion of their diet from gleaning tree bark and associated habitats (Banko and Banko 2009, Hooper and Lennartz 1981, Jackson 1979, Mariani and Manuwal 1990), but care must be taken when making "prey availability" designations (Cooper and Whitmore 1990, Wolda 1990), especially when management recommendations are based on the findings. A factor usually not taken into account when considering forest management practices for birds is how the implementation of these practices affect food availability. Alterations to forested habitats from timber harvests (Duguay et al. 2000, Niemelä et al. 1993, Ulyshen et al. 2006), prescribed fire (Campbell et al. 2007, Hanula and Wade 2003, Harper et al. 2000), invasive plants (Hanula and Horn 2011, Hudson et al. 2013, Tallamy 2004), and dead wood manipulations (Hanula et al. 2006, Horn and Hanula 2008, Siitonen 2001, Ulyshen and Hanula 2009) can all have impacts on the invertebrate communities residing there and likely their avian predators as well.

Results from this study show that invertebrate communities residing on loblolly pine can vary with height on tree trunks. Despite finding higher numbers and weights of total arthropods on lower trunk sections, these values were predictive of values further up the tree, although more intensive sampling is needed to draw definite conclusions. More specifically, wood roach biomass showed a strong correlation between the two bole sections. Due to their abundance and importance to the food web, trunk arthropods should serve as model organisms for detecting environmental change. Many techniques have been used to collect arthropods on tree trunks and each have advantages and disadvantages. In particular, passive traps (crawl traps and sticky traps) collect arthropods continuously, including times when birds are not active. Our findings indicate that sampling the lower bole with fast-acting insecticides to the lower, accessible part of tree boles is a useful tool for rapidly assessing arthropods and is representative of the whole bole. However, future research that incorporates increased sample sizes in different locales is necessary to help further explain the relationship of arthropod density and biomass vertically along tree boles. Efforts should focus on developing equations describing the relationship between arthropods on lower tree trunks and those higher up the tree. The result would be more confident predictions of prey availability that could help determine how forest management practices are affecting bark-foraging birds.

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