

# The importance of forest type, tree species and wood posture to saproxylic wasp (Hymenoptera) communities in the southeastern United States

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**Abstract** Although the forests of the southeastern United States are among the most productive and diverse in North America, information needed to develop conservation guidelines for the saproxylic (i.e., dependent on dead wood) fauna endemic to the region is lacking. Particularly little is known about the habitat associations and requirements of saproxylic parasitoids even though these organisms may be even more vulnerable than their hosts. We sampled parasitoids emerging from dead wood taken from two forest types (an upland pine-dominated forest and a lowland hardwood-dominated forest), three tree species (*Liquidambar styraciflua* L., *Pinus taeda* L., and *Quercus nigra* L.) and two wood postures (standing dead trees (i.e., snags) and fallen logs) in South Carolina. Parasitoid abundance did not differ between forest types or among tree species, but did differ between wood postures, being higher in snags than logs. This difference may have been due to the logs being in contact with the ground or surrounding vegetation and therefore less accessible to parasitoids. Parasitoid abundance and density decreased with height on both snags and logs. Species richness did not differ between forest types, among tree species or between wood postures. According to analysis of similarities, parasitoid communities did not differ between forest

types, but did differ among tree species. The wasp communities associated with the different tree species and posture combinations were distinct. In addition, communities associated with the upper boles and crowns of snags were distinct from those occurring lower on snags. These results emphasize the importance of maintaining tree diversity in managed forests as well as retaining or creating entire snags at the time of harvest.

**Keywords** Biodiversity · Canopy · Coarse woody debris · Vertical distribution · Vertical stratification

## Introduction

Parasitic wasps are among the most taxonomically diverse and ecologically important insects (Gaston 1991; LaSalle 1993). Unfortunately, they are also among the least well known and remain largely disregarded in the field of insect conservation (Shaw and Hochberg 2001). This neglect is particularly alarming considering the vulnerabilities of the group. Their high degree of host specificity, high trophic level, chronically low population sizes, dependence on unreliable resources, haplodiploid sex determination, and sensitivity to habitat fragmentation and other environmental changes make them especially extinction prone (LaSalle and Gauld 1991; LaSalle 1993; Kruess and Tschamtké 1994; Jonsell et al. 1999; Shaw and Hochberg 2001).

The diverse saproxylic fauna, consisting of all organisms directly or indirectly dependent on dead or dying wood, is perhaps the most imperiled functional group in managed forests (Siitonen 2001; Grove 2002). Many studies have investigated the habitat requirements of saproxylic beetles in the past several decades, but those of saproxylic parasitic wasps remain mostly unknown (but see

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Hilszczański et al. 2005; Vanderwel et al. 2006; Hedgren 2007; Gibb et al. 2008; Stenbacka et al. 2010) even though they may be even more species rich (Siitonen 2001) and interact in more complex ways with other members of the saproxylic community (LaSalle and Gauld 1991). The best studied saproxylic organisms, such as bark beetles and other economically important forest pests, are known to be attacked by “parasitoid complexes” consisting of multiple species. For example, Berisford et al. (1971) found 12 parasitoid taxa attacking four species of *Ips* in Virginia. Such complex interactions are thought to regulate host populations, stabilize ecosystems and maintain biodiversity (LaSalle 1993), underscoring the importance of this understudied fauna.

Understanding the distribution patterns and habitat requirements of parasitic wasps associated with wood is an important first step in developing conservation guidelines for the group. In theory, host distribution patterns should be useful in predicting the habitat associations of parasitoids. Many beetle hosts in the southeastern United States, for example, exhibit strong preferences for particular forest types, tree species and wood postures (Ulyshen and Hanula 2009). While the distribution patterns of parasitic wasps are no doubt similar, the host ranges of most species are largely or entirely unknown, making such predictions difficult or impossible. Furthermore, the distribution patterns of parasitic wasps are likely much narrower than those of their hosts. Specific substrate requirements, for instance, may limit parasitoid occurrence to a small portion of the host distribution. For example, hosts beneath thick bark may be unavailable to parasitoid species possessing short ovipositors. Such species may be restricted to the relatively thin bark of small diameter trees or to the uppermost portions of large trees. Ball and Dahlsten (1973), for example, showed that parasitism rate increased with decreasing diameter, a correlate of bark thickness, in *Pinus* in California.

Parasitoid communities associated with standing dead trees (i.e., “snags”) are often vertically stratified. For example, Vanlaerhoven and Stephen (2002) found some parasitic wasp species associated with *Dendroctonus frontalis* in the southeastern United States are most abundant near the middle of the bole whereas others prefer the upper bole. Similarly, Dahlsten and Stephen (1974) found most parasitic wasps species associated with *D. ponderosae* Hopkins in California to be concentrated high on the bole. Also, in Sweden, Hedgren (2007) compared parasitoids from low (30–40 cm tall) and high (4 m tall) stumps. Parasitoid frequency, density and diversity were higher at 1.5 m on high stumps than at the base of high stumps or in low stumps and many species were more strongly associated with high stumps than low stumps. To our knowledge, no studies have compared the distribution patterns of parasitoids in intact snags and fallen trees. If distribution patterns are governed

largely by bark thickness, there may be few differences between the two postures. Other factors known to vary between standing and fallen trees, however, may also be important, such as humidity and sun exposure. In addition, parasitoid species foraging for honeydew in the canopy may be more likely to parasitize hosts high on the boles of snags (Vanlaerhoven and Stephen 2002) and may be distributed differently on fallen trees. Hilszczański et al. (2005) sampled parasitoids from 3 m tall stumps and 4 m long logs placed on the ground in Sweden. Two common species were recovered only from the stumps, suggesting some parasitoid species may be restricted to snags.

Because many parasitoid species are specific to particular insect hosts and these, in turn, are often specific to particular tree hosts, parasitoid communities are likely to differ greatly among tree species. This is particularly true at early stages of decay when tree specificity among insect hosts tends to be highest. In some cases, however, parasitoid community composition may vary among tree species even if host availability does not. For example, DeLeon (1935) found that *Coeloides dendroctoni*, the most important parasitoid of *Dendroctonus monticolae* in the western United States, would not attack *D. monticolae* within western yellow pine. Similarly, Ball and Dahlsten (1973) sampled parasitoids attacking *Ips paraconfusus* infesting (at similar densities) both *Pinus ponderosa* and *P. lambertiana* in a single forest in California. Of the ten species collected overall, five were only recovered from *P. lambertiana*, one of them being very abundant. Furthermore, the percentage of hosts parasitized was consistently higher in *P. lambertiana* than in *P. ponderosa*, even for parasitoid species that utilized hosts in both tree species. The authors attribute these results to the fact that *P. ponderosa* has thicker bark. Ball and Dahlsten (1973) also showed that some parasitoids strongly prefer smooth bark, another feature likely to vary among tree species.

Given that tree species are not distributed evenly among forests, forest type is another factor likely to affect parasitoid community composition. In addition, differences in temperature, humidity and other environmental conditions among forests may also affect the distribution patterns of this sensitive fauna. For example, in Sweden, Gibb et al. (2008) attributed changes in saproxylic parasitoid assemblages in part to relatively small differences in climate between coastal and inland sites. Although, to our knowledge, previous studies have not compared parasitoid communities among forest types, there have been efforts to compare parasitoid communities among forests with different management histories. For example, in Sweden, Hilszczański et al. (2005) sampled parasitoids from dead spruce in old-growth forests, mature managed forests and previously forested sites that had recently been clear cut. Even though the wood sampled in the different forests were of the same origin, the parasitoid communities in clear cuts

were significantly distinct from those in old-growth or mature managed forests. These results demonstrate that microclimate plays an important role in determining the composition of parasitoid communities.

In a recent project comparing beetle communities among two forest types (an upland pine-dominated forest and a lowland hardwood-dominated forest), three tree species (*Liquidambar styraciflua* L., *Pinus taeda* L., and *Quercus nigra* L.) and two wood postures (standing snags and fallen logs) in the southeastern United States (Ulyshen and Hanula 2009), a large number of parasitic wasps were collected. These data, presented here, provide an excellent opportunity to better understand the distribution patterns and habitat requirements of these poorly known and potentially imperiled insects.

## Methods

### Study site

The project took place on the Department of Energy Savannah River Site (SRS), a National Environmental Research Park located on the upper Coastal Plain Physiographic Province of South Carolina. Most of the land on the SRS was formerly used for agricultural purposes and most forests currently standing were planted or regenerated in the early 1950s (Kilgo and Blake 2005). The SRS is primarily pine-dominated forests growing on relatively dry upland sites and hardwood-dominated forests occupying swamps and riparian lowlands (Kilgo and Blake 2005). At least three tree species are relatively common in both forest types. Sweetgum (*L. styraciflua*) and water oak (*Q. nigra*) grow most commonly on mesic sites dominated by mixed hardwoods but also appear sporadically among pines on dry upland sites. Similarly, loblolly pine (*P. taeda*) is currently the dominant pine species growing in upland pine forests but was historically restricted to moist lowland sites (Schultz 1997) and continues to grow there at low densities.

The upland and lowland forests used in this study were approximately 25 km apart. One Hobo Data Logger was placed in each forest type for approximately 1 year (2006–2007) to continuously record temperature and humidity. On average, the upland forest was warmer than the lowland forest (18.8 and 17.8°C, respectively) whereas relative humidity was on average lower there than in the lowland forest (72.2 and 76.6%, respectively). These differences were most pronounced during the growing season.

### Sampling design

Our sampling followed a  $2 \times 3 \times 2$  factorial design with the respective factors being forest type (upland pine forest

vs. lowland hardwood forest), tree species (*L. styraciflua* vs. *P. taeda* vs. *Q. nigra*), and posture (log vs. snag). There were three replicates.

On June 5–6 2006 we created nine snags and nine logs in the upland sites and the same number in the lowland sites, equally divided among *L. styraciflua*, *P. taeda*, and *Q. nigra* (i.e., three snags and logs of each species at each site). Snags were created by girdling the trees to a depth of 3 cm or more using a chainsaw and spraying full strength (53.8%) glyphosate (Foresters'®, Riverdale Chemical Company, Burr Ridge, IL) into the wounds. To prevent the herbicide from traveling up the tree and possibly affecting insect colonization, a second girdle was created about 15 cm above the first before herbicide was applied. Only the lower girdle was treated. All girdled trees examined 2 weeks after treatment were dead.

Approximately 11 months later, in May 2007, we returned to collect sections from the three logs and snags of each species at each site. After felling the snags with chainsaws, we removed 0.5 m sections from the lower bole, middle bole, and upper bole of each snag and log. The position of each section was measured from the tree base (for details, see Ulyshen et al. 2009). We also collected three 0.5 m crown sections taken from major limbs or sometimes the upper-most portion of the main bole. The tops of all but one of the *L. styraciflua* snags had broken, so those crown sections had been in contact with the ground for an unknown length of time. The upper bole sections from these trees were taken directly below the point of breakage. All the other snags were intact. All bole and crown sections cut on a given day (May 3 and 8 for upland and lowland forests, respectively) were labeled and transported to Athens, Georgia.

We recorded the diameter (measured at the center) and bark coverage (visual estimation) of each bole and crown section in the laboratory. We used these data to calculate the total surface area (not including ends) and bark surface area (product of surface area and visual estimate of bark coverage) sampled from each snag and log. Wood surface area sampled did not vary significantly between forest types, among tree species or between wood postures, but bark surface area varied significantly among tree species, being lower for *P. taeda* than for *Q. nigra* and *L. styraciflua* (Ulyshen and Hanula 2009). There was also a significant interaction between tree species and posture due to the fact that *P. taeda* snags had less bark than *P. taeda* logs (Ulyshen and Hanula 2009).

Over a 20 week period, emerging insects were collected in the laboratory using rearing bags (Ulyshen and Hanula 2009), one of the most efficient methods for collecting insects from dead wood (Jonsell and Hansson 2007). All parasitic wasps collected were identified to the lowest taxonomic level possible. Taxa not identified to species were assigned to morphospecies.

## Data analysis

Bole and crown samples from each snag or log were combined before conducting analyses of covariance on the three-way factorial design (SAS Institute 1990). Surface area and bark surface area were the covariates and the main effects were forest type, tree species and wood posture. All effects were fixed and there were no missing or incomplete samples. The response variables were morphospecies richness and  $\log(x + 1)$ -transformed abundance data.

To compare community composition between forest types, among tree species and between wood postures, analyses of similarities (ANOSIM) were carried out on  $\log(x + 1)$ -transformed abundance data using PAST (Hammer et al. 2001) with 10,000 permutations using a Bray-Curtis distance measure. These analyses produce  $R$  and  $P$  values with large positive values of  $R$  (up to 1) and low values of  $P$  (e.g.,  $<0.05$ ) signifying dissimilarity among or between wasp communities. The data matrix used in these analyses consisted of 36 samples representing the 36 trees (i.e., the four positions sampled on each tree were combined for these analyses). Analyses of similarities were also carried out separately for each tree species on  $\log(x + 1)$ -transformed density (i.e., abundance/wood surface area) data to compare community composition among the eight posture and position combinations. Each of the data matrices used in these analyses consisted of 48 samples representing the 48 posture and position combinations for each tree species. Because we thought gregarious parasitoid taxa may strongly influence these results, all of the ANOSIM analyses mentioned above were repeated using presence/absence data and a Jaccard distance measure.

Indicator species analyses (Dufrêne and Legendre 1997) were performed using PC-ORD (McCune and Mefford 2006) to determine which morphospecies were significantly associated with a particular (1) forest; (2) tree species and posture combination; (3) posture and position combination. The dataset used in these analyses consisted of 51 morphospecies after excluding those found in fewer than three samples. Indicator values ranging from 0 (no association) to 100 (perfect association) were tested for statistical significance ( $P < 0.05$ ) using a Monte Carlo randomization with 4,999 permutations (McCune and Grace 2002).

## Results

### Abundance and richness

In total, 2,069 wasps from 23 families and 157 morphospecies were collected (Table 1). Wasp abundance did not differ between forest types or among tree species, but did differ between wood postures (Table 2), being higher in

**Table 1** Number of wasp morphospecies and individuals collected by family from snags or logs of three tree species in two forest types

Family	No. morphospecies	No. individuals
Aphelinidae	1	1
Aulacidae	1	21
Bethylidae	9	407
Braconidae	41	300
Ceraphronidae	7	69
Chalcididae	2	4
Crabronidae	1	1
Diapriidae	7	68
Dryinidae	3	3
Encyrtidae	11	520
Eucharitidae	1	3
Eucoilidae	4	12
Eulophidae	16	242
Eupelmidae	6	24
Eurytomidae	2	3
Ichneumonidae	11	18
Megaspilidae	1	2
Mymaridae	5	140
Platygastridae	11	49
Pompilidae	2	2
Pteromalidae	13	173
Signiphoridae	1	6
Sphécidae	1	1
Total	157	2069

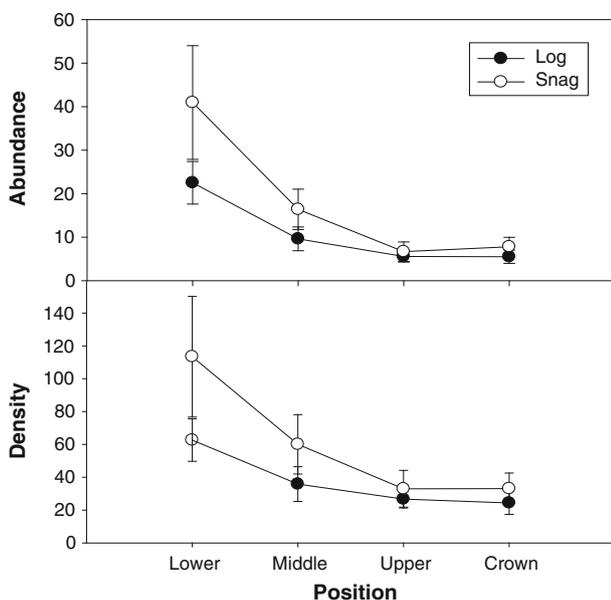
snags than logs (Fig. 1). Wasp abundance and density decreased with height on both snags and logs (Fig. 1). Abundance and density were consistently higher in snags throughout the lengths of the trees, although these differences were marginal high on the trees (Fig. 1). Wasp richness did not differ between forest types, among tree species or between wood postures (Table 2).

### Community composition

According to ANOSIM, wasp communities did not differ between forest types ( $R = -0.02$ ,  $P = 0.60$ ), but did differ among tree species ( $R = 0.6$ ,  $P < 0.01$ ). With one exception, the wasp communities associated with the different tree species and posture combinations were all significantly distinct from one another (Table 3). For *P. taeda*, the wasp community collected from the crowns of logs was distinct from that collected from the lower boles of logs (Table 4). The community collected from the crowns of snags was distinct from all other snag positions and the community collected from the upper boles of snags was distinct from that collected from the lower boles of snags. The wasp community collected from mid boles of logs was distinct

**Table 2** Results for analyses of covariance on the three-way factorial design with log(x + 1)-transformed abundance and species richness as the response variables

Source	Abundance				Richness		
	df	MS	F	P	MS	F	P
Forest type	1	0.07	0.73	0.40	11.86	0.65	0.43
Tree species	2	0.14	1.41	0.26	16.03	0.88	0.43
Wood posture	1	0.55	5.44	0.03	27.28	1.49	0.23
Forest type × tree species	2	0.00	0.01	0.99	0.88	0.05	0.95
Forest type × wood posture	1	0.32	3.17	0.09	4.87	0.27	0.61
Tree species × wood posture	2	0.26	2.58	0.10	53.89	2.95	0.07
Forest type × tree species × wood posture	2	0.02	0.16	0.86	15.93	0.87	0.43
Surface area (covariate)	1	0.02	0.20	0.66	6.88	0.38	0.55
Bark surface area (covariate)	1	0.39	3.85	0.06	77.94	4.27	0.05
Error	22	0.10			18.25		
Total	35						



**Fig. 1** Wasp abundance and density (abundance/m<sup>2</sup> wood surface) at four positions (lower bole, middle bole, upper bole and crown) on standing (snags) and downed (logs) dead trees

from that collected from the mid boles of snags. For *Q. nigra*, the wasp communities collected from the crowns and upper boles of logs were distinct from that collected

from the lower boles of logs (Table 4). Similarly, the communities collected from the crowns and upper boles of snags were distinct from that collected from the lower boles of snags. The wasp community collected from lower boles of logs was distinct from that collected from the lower boles of snags. For *L. styraciflua*, the wasp community collected from the crowns of logs was distinct from those collected from mid boles or lower boles of logs (Table 4). The community collected from the crowns of snags was distinct from all other snag positions. The wasp community collected from the crowns of logs was distinct from that collected from the crowns of snags. These findings did not change appreciably when the analyses were performed on presence/absence data (results not shown).

Based on indicator species analysis, only three of the 51 morphospecies were significantly associated with a particular forest type (two with the upland forest, one with the lowland forest), about the number expected by chance at the 0.05 level of significance. In contrast, 24 (i.e., nearly half) of the morphospecies were significantly associated with a particular tree species and posture combination: seven with *Q. nigra* snags, five with *Q. nigra* logs, four each with *P. taeda* snags and logs, three with *L. styraciflua* logs and one with *L. styraciflua* snags. In addition, nine morphospecies were significantly associated with a particular posture and position combination; three with the

**Table 3** Analysis of similarities (ANOSIM) based on log(x + 1)-transformed abundance data for each tree species and posture combination

	<i>Q. nigra</i> log	<i>Q. nigra</i> snag	<i>P. taeda</i> log	<i>P. taeda</i> snag	<i>L. styraciflua</i> log
<i>Q. nigra</i> snag	<b>&lt;0.01</b>	–	–	–	–
<i>P. taeda</i> log	<b>&lt;0.01</b>	<b>&lt;0.01</b>	–	–	–
<i>P. taeda</i> snag	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	–	–
<i>L. styraciflua</i> log	0.09	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	–
<i>L. styraciflua</i> snag	<b>0.01</b>	<b>0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.01</b>

P-values are given for each pairwise comparison. Significant values ( $P < 0.05$ ) are given in bold

**Table 4** Analysis of similarities (ANOSIM) based on  $\log(x + 1)$ -transformed density (abundance/surface area) data for each posture  $\times$  position combination

		Log crown	Log lower	Log middle	Log upper	Snag crown	Snag lower	Snag middle
<i>P. taeda</i>								
Log lower	<b>0.01</b>	–	–	–	–	–	–	–
Log middle	0.13	0.71	–	–	–	–	–	–
Log upper	0.35	0.89	0.88	–	–	–	–	–
Snag crown	0.15	<b>0.01</b>	0.06	0.06	–	–	–	–
Snag lower	<b>0.01</b>	0.10	0.41	0.31	<b>&lt;0.01</b>	–	–	–
Snag middle	<b>&lt;0.01</b>	<b>0.02</b>	<b>0.02</b>	<b>0.01</b>	<b>&lt;0.01</b>	0.09	–	–
Snag upper	<b>0.05</b>	<b>0.03</b>	0.06	0.14	<b>0.01</b>	<b>0.03</b>	0.60	–
<i>Q. nigra</i>								
Log lower	<b>0.02</b>	–	–	–	–	–	–	–
Log middle	0.35	0.41	–	–	–	–	–	–
Log upper	0.76	<b>0.03</b>	0.37	–	–	–	–	–
Snag crown	0.16	<b>0.01</b>	<b>&lt;0.01</b>	<b>0.05</b>	–	–	–	–
Snag lower	<b>0.01</b>	<b>0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.01</b>	–	–	–
Snag middle	0.09	0.17	0.16	0.26	0.21	0.44	–	–
Snag upper	<b>0.02</b>	<b>0.01</b>	0.04	0.06	0.12	<b>0.02</b>	0.87	–
<i>L. styraciflua</i>								
Log lower	<b>0.02</b>	–	–	–	–	–	–	–
Log middle	<b>0.02</b>	0.89	–	–	–	–	–	–
Log upper	0.22	0.90	0.71	–	–	–	–	–
Snag crown	<b>0.02</b>	<b>0.01</b>	<b>0.01</b>	<b>0.02</b>	–	–	–	–
Snag lower	<b>0.01</b>	0.40	0.39	0.35	<b>0.01</b>	–	–	–
Snag middle	<b>0.01</b>	0.85	0.75	0.60	<b>&lt;0.01</b>	0.66	–	–
Snag upper	<b>0.04</b>	0.27	0.45	0.41	0.16	0.26	0.42	–

*P*-values are given for each pairwise comparison. Significant values ( $P < 0.05$ ) are given in bold

lower boles of logs, two with the crowns of logs, two with the lower boles of snags, one with the crowns of snags and one with the mid boles of snags. Taxa identified to genus or species found to be significantly associated with a particular habitat are listed in Table 5.

## Discussion

We found no differences in wasp abundance, richness and composition between upland and lowland forests, suggesting the climatic differences between the two forest types were not enough to appreciably affect parasitoid communities. Only three tree species common to both forests were sampled in this study, so it cannot be concluded that the overall assemblages in the two forest types are the same. In fact, it seems likely that wasp community composition differs greatly between the upland and lowland forests considering that lowland forests support many tree species not found in upland forests and we found wasp communities to vary greatly among tree species.

Although parasitoid abundance and richness did not vary among tree species and varied little between wood postures, community composition was strongly influenced

by both factors. Nearly half of the most frequently collected taxa were significantly associated with a particular tree species and posture combination. In addition, one-sixth of the most frequently collected taxa were significantly associated with a particular posture and position combination. These results are likely due to differences in host availability as well as to differences in important substrate characteristics and environmental conditions such as bark thickness, temperature and humidity. Because all taxa identified to genus level or below appear to have broad host ranges (Table 5) and little information is available on other aspects of their life histories, we are unable to account for the significant habitat associations observed in this study. These distribution patterns may be explained as additional information becomes available in the future.

Overall, parasitoids were significantly more abundant in snags than in logs, but this may be largely due to the logs being in contact with the ground or surrounding vegetation and therefore less accessible to parasitoids. In contrast, the entire circumference would have been available to parasitoids on snags. Support for this comes from the fact that the difference in abundance between snags and logs was greatest low on the bole where logs would have been most likely in contact with the ground (Fig. 1).

**Table 5** Known host associations and results from indicator species analysis (indicator value, IV, and *P* value) for parasitoid taxa identified to genus level or below

Species	Host/habitat associations	
	Previous studies	This study
<b>Aulacidae</b>		
<i>Pristaulacus niger</i> (Shuckard)	Associated with <i>Pinus</i> (Townes, 1950), probably Cerambycidae (Haack and Wilkinson, 1987)	Mid bole (IV = 13.1, <i>P</i> = 0.04) of <i>P. taeda</i> snags (IV = 36.4, <i>P</i> < 0.01)
<b>Braconidae</b>		
<i>Cenocoelius</i> sp.	Curculionidae, Cerambycidae, Buprestidae (wood- and bark-borers) (van Achterberg, 1997)	Crowns (IV = 30.8, <i>P</i> < 0.01) of <i>L. styraciflua</i> snags (IV = 17.4, <i>P</i> < 0.01)
<i>Doryctes erythromelas</i> (Brullé)	Cerambycidae and Curculionidae including <i>Xylotrechus colonus</i> (Fabricius) (Yu 2010)	Upland pine-dominated forest (IV = 9.8, <i>P</i> = 0.03)
<i>Ecphyllus unifasciatus</i> Marsh	Many curculionids, mostly Scolytinae; one cerambycid and several bostrichids (Yu 2010)	Crowns (IV = 26, <i>P</i> < 0.01) of <i>L. styraciflua</i> logs (IV = 17.8, <i>P</i> < 0.01)
<i>Heterospilus</i> sp 2	Mostly wood-boring beetles but some sawflies and moths (Marsh, 1997)	<i>P. taeda</i> snags (IV = 22.2, <i>P</i> < 0.01)
<i>Heterospilus</i> sp 4	Mostly wood-boring beetles but some sawflies and moths (Marsh, 1997)	Crowns of logs (IV = 12.7, <i>P</i> = 0.04)
<i>Orgilus</i> sp.	Mostly microlepidoptera (Yu 2010)	Lower bole (IV = 16.4, = 0.01) <i>Q. nigra</i> logs (IV = 20.1, <i>P</i> < 0.01)
<i>Wroughtonia</i> sp.	Buprestidae, Bostrichidae and Curculionidae (Yu 2010)	<i>Q. nigra</i> snags (IV = 30.3, <i>P</i> < 0.01)
<b>Diapriidae</b>		
<i>Trichopria</i> sp.	Various Diptera (esp. tephritids and calyprate muscoids); hyperparasitoids of some symphytans, Coleopterans, and Lepidopterans (Yoder 2010)	Lower boles (IV = 12.4, <i>P</i> = 0.05) of <i>P. taeda</i> logs (IV = 22.5, <i>P</i> < 0.01)
<b>Pteromalidae</b>		
<i>Spalangia</i> sp.	Dipteran puparia; rarely hyperparasitoid (Gibson, 2009)	<i>Q. nigra</i> logs (IV = 20.9, <i>P</i> < 0.01)

### Conservation implications

Although the forests of the southeastern United States are among the most important to timber production and biodiversity in North America, few efforts have been made to develop conservation guidelines for saproxylic organisms endemic to the region, and this is the first to focus on the saproxylic parasitoid community. Two important conclusions can be reached from this study. First, parasitoid community composition varied greatly among tree species, underscoring the importance of protecting tree diversity in managed landscapes. Second, parasitoid communities in snags and logs were different, adding to the growing body of evidence that snags support distinct insect communities and are of considerable conservation value (e.g., Jonsell et al. 1998; Sverdrup-Thygeson and Ims 2002; Kappes and Topp 2004; Hedgren and Schroeder 2004; Franc 2007; Ulyshen and Hanula 2009). In addition, we found parasitoid communities associated with the upper boles and crowns of snags to be distinct from those associated with the lower boles of snags. These findings indicate that entire snags should be retained or created in managed forests as

opposed to the practice, now common in some countries (e.g., Jonsell et al. 2004), of creating 4–5 m tall stumps at the time of harvest.

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