

# Patterns of saproxylic beetle succession in loblolly pine

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- Abstract**
- 1 Patterns of insect succession in dead wood remain unclear, particularly beyond the first several years of decay. In the present study, saproxylic beetles were sampled from loblolly pine (*Pinus taeda* L.) logs aged between 1 month and 9 years old using both emergence traps attached to logs in the field and rearing bags in the laboratory.
  - 2 Species richness peaked within the first year as a result of a diverse assemblage of bark beetles, wood-borers and predators associated with young logs. After the phloem phase, there were no significant differences in species richness among decay classes.
  - 3 Beetle communities differed significantly among decay classes, with 25 and seven species being significantly associated with young and old logs, respectively.

**Keywords** Arthropods, biodiversity, coarse woody debris, coleoptera, conservation, forest management, species turnover.

## Introduction

By contrast to rapidly degrading substrates such as carrion and dung, wood decays slowly, often requiring decades or even centuries to decompose completely, and cannot be studied easily from beginning to end. Beetle community composition changes during wood decay in a predictable fashion. Although the details of this succession remain poorly understood, particularly at advanced stages of decay, the process can be partitioned into three overlapping phases (Savely, 1939). (i) *Phloem phase*: The first beetles to colonize dead wood are phloem feeders and their predators. These beetles quickly consume the carbohydrate-rich phloem layer, causing the bark to separate from the wood. Because phloeophagous beetles must cope with the chemical defenses of recently-killed trees, they are often highly host specific. (ii) *Subcortical space phase*: The subcortical space resulting from the activities of the phloem-feeding beetles is rapidly colonized by fungus and a diverse assemblage of beetles specialized for life under bark. This phase ends within months or years when the bark finally falls away from the wood. Because subcortical beetles are usually mycophagous or predatory and do not feed on the wood itself, they are generally less species specific than phloem feeders (Elton, 1966). (iii) *Rot phase*: As decomposition proceeds, wood becomes increasingly infiltrated by fungi. The beetle communities consequently become increasingly dominated by mycophages and their predators. The beetles

inhabiting wood at these more advanced stages are the least specific to particular tree species (Howden & Vogt, 1951).

How insect species richness changes during the decay process is poorly understood. It may either increase with more advanced decay classes in response to the diversification of wood-rotting fungi and increased microhabitat diversity (Langor *et al.*, 2008) or decrease in response to declining nutritional quality after the loss of phloem (Howden & Vogt, 1951; Siitonen, 2001). This question remains largely unresolved because few efforts have been made to sample insects from a sufficiently wide range of age classes under carefully controlled experimental conditions.

Interest in saproxylic beetles has increased recently in response to evidence that many species are at risk of disappearing in intensively managed forests. Although it is clearly important to protect wood throughout the decay process, the vulnerabilities of species may differ among different stages of decay. For example, species associated with the phloem phase are often highly host specific (Langor *et al.*, 2008), emphasizing the importance of protecting tree diversity in managed forests. However, these species may be less sensitive to habitat fragmentation than species associated with later stages of decay. Phloem is quickly consumed in a dead tree, requiring rapid detection and colonization. By contrast, the nature of dead wood at later stages of decay is probably more permanent, making strong dispersal powers less important. For example, studies conducted in Scandinavia have shown that bark beetles (i.e. early colonists) can fly long distances to colonize freshly-killed wood (Nilssen, 1984) and are little affected

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by forest management (Johansson *et al.*, 2006). Furthermore, beetles associated with brown rot in large-diameter logs have been shown to have relatively poor dispersal powers in Tasmania (Yee *et al.*, 2006) and most endangered species in Europe are associated with wood in advanced stages of decay (Langor *et al.*, 2008). Because beetle species inhabiting wood at later stages of decay may be among the most vulnerable, it is important to become better acquainted with this still poorly known community, particularly in commercially important (i.e. intensively managed) tree species such as loblolly pine.

Loblolly pine (*Pinus taeda* L.) has largely displaced longleaf pine (*Pinus palustris* Mill.) throughout the southeastern U.S.A. and is currently one of the most intensively managed timber trees in North America (Schultz, 1997). Yet, patterns of beetle succession in loblolly pine remain largely unknown. Barber and Van Lear (1984) determined that 50% of loblolly pine slash in Piedmont South Carolina should disappear after 10 years, 90% after 32 years and 99% after 64 years. Beetle succession has only been studied for the first year or two (Graham, 1925; Overgaard, 1968; Moser *et al.*, 1971; Hines & Heikkinen, 1977) of this >64-year process. In the present study, we document changes in the richness and composition of beetles during the first 9 years of decay in South Carolina.

## Materials and methods

### Study site

This research took place on the 80 267-ha Savannah River Site (SRS) located in the upper Coastal Plain Physiographic Province of South Carolina. The SRS, a facility owned and operated by the U.S. Department of Energy, was established in 1951, and was designated an Environmental Research Park in 1972 (Kilgo & Blake, 2005). Most of the land now owned by the Savannah River site was formerly used for agricultural purposes and most forests currently standing, including those used in the present study, were planted in the early 1950s (Kilgo & Blake, 2005). Loblolly pine was the dominant tree species, although several other species, including water oak (*Quercus nigra* L.) and sweetgum (*Liquidambar styraciflua* L.), were also present at low densities. The understory was generally dominated by wax myrtle (*Myrica cerifera* L.), blackberry (*Rubus* spp.), kudzu (*Pueraria montana* (Lour.) Merr.), *Lespedeza bicolor* Turcz. and Japanese honeysuckle (*Lonicera japonica* Thunb.).

### Insect sampling

This was a two-part project, using different methods to collect insects emerging from loblolly pine (*P. taeda* L.) logs. The first method, termed 'on-location sampling', involved trapping insects directly from logs in the field. The second method, termed 'off-location sampling', involved removing sections from the logs and transporting them to a rearing facility located in Athens, Georgia. The trees used in this study were planted in the early 1950s and were felled in: August 1997 ('old' logs), August 2001 ('middle-aged' logs) and May 2005 ('young' logs).

*On-location sampling.* On-location sampling was conducted using a completely randomized block design with four blocks



**Figure 1** (A) Rearing bags used for off-location sampling. (B) Old logs sampled off-location were held together with plastic fencing material. (C) Emergence trap used for on-location sampling; (note that the image is not from the present study).

(Ulyshen & Hanula, 2009b). Emergence traps (Fig. 1C) were installed on four logs of each age class in each block (i.e. 12 logs per block and 48 traps in total). Each emergence trap consisted of black cotton canvas wrapped around a log and attached to a clear polyvinyl chloride (PVC) pipe (length 101 cm, outer diameter 11.4 cm, inner diameter 10.2 cm; Excalibur Extrusions Inc., Placentia, California) (Fig. 1C). Emerging beetles entered the pipe through an opening (84 × 6 cm) facing the log. The section of pipe removed to create this opening was attached above the opening with three wing-nuts (Fig. 1C). One end of the pipe was capped. The other end led, via a PVC elbow connector, to a collecting jar filled with propylene glycol (Fig. 1C). The pipe was supported by positioning the opening over a pair of long nails driven at angles into one side of the log. Additional nails were driven into the top and opposite side of the log to create a space between the log and the cloth. The cloth was fastened to the pipe below the opening with closely-spaced screws. After wrapping the cloth around the log, the loose end of cloth was pinched between the pipe and the piece of pipe removed to create the opening using three wing-nuts (Fig. 1C). The cloth was then tightly bound to the log on each side of the pipe with metal wire. The average length of wood enclosed within the traps, as measured by the distance between the wires, was 1.12 m. When logs were in contact with the soil, shovels were used to create a space through which to pass the cloth. Some of the oldest logs were too decayed to support the traps using nails. In such cases, sections of wood

were removed and enclosed within traps by tying off the two ends of cloth. We sampled continuously from 7 June 2005 to 16 March 2006. At the time of sampling, the logs were aged 1–10 months, 46–55 months and 94–103 months for young, middle-aged and old logs, respectively.

**Off-location sampling.** Sections were removed from 12 logs, four from each of the three age classes (16, 60 and 108 months for young, middle-aged and old logs, respectively), on 8 August 2006. Chainsaws were used to remove three 0.5-m sections from each log for a total of 36 sections. The three sections taken from each log were separated by approximately 5 m with the first section coming from near the base of the tree. Sections from old logs were kept intact by tightly wrapping them in plastic fencing material (square mesh, diameter 4.5 cm) (Fig. 1B). Some sections were taken from logs used in on-location sampling, although we did not remove sections that had been enclosed within the emergence traps. All sections were transported to a rearing facility in Athens, Georgia. Emerging beetles were collected using rearing bags (Ulyshen & Hanula, 2009a) for approximately 8 months (8 August 2006 to 5 April 2007).

Beetles collected from both on- and off-location sampling were stored in 70% ethanol and later identified to the lowest taxonomic level possible using the classification system of Arnett and Thomas (2001, 2002). Voucher specimens have been deposited in the Georgia Museum of Natural History, Athens, Georgia.

### Statistical analysis

We used PAST (Hammer *et al.*, 2001) to perform analysis of similarities with 10 000 permutations using a Bray–Curtis distance measure to quantitatively compare communities among the three age classes for on- and off-location sampling. Only species present in three or more samples (i.e. 85 and 40 species for on- and off-location sampling, respectively) were included in the datasets. Indicator species analyses were performed using PC-ORD (McCune & Mefford, 2006) on the same datasets to identify species significantly associated with the different decay classes.

Analysis of variance was used to compare species richness among young logs, middle-aged logs and old logs for both on- and off-location sampling (SAS Institute, 1990). For off-location sampling, data from the three sections removed from each log were combined before analysis.

### Results

Overall, we collected 10 506 beetles from 44 families and 209 species (Appendix 1). Almost twice as many species were collected on-location than off-location (178 and 91 species, respectively).

On the basis of analysis of similarities, beetle community composition differed significantly among decay classes for both on- ( $R = 0.63$ ,  $P = 0.0003$ ) and off- ( $R = 0.78$ ,  $P < 0.0001$ ) location sampling. According to indicator species analysis, 25 and seven species were significantly associated with young and old logs, respectively (Table 1). Those associated with the young logs primarily consisted of phloem associates (i.e. bark

**Table 1** Beetle species significantly associated with certain decay classes of mature loblolly pine in a southeastern U.S. forest based on indicator species analysis

	Indicator value (on/off- location)	P-value
<b>Young log associates</b>		
<i>Acanthocinus nodosus</i> (Fabricius)	25 (on)	0.025
<i>Acanthocinus obsoletus</i> (Olivier)	93.7 (on)	0.001
<i>Cerylon unicolor</i> (Ziegler)	31.2 (on)	0.006
<i>Clavilispinus</i> sp.	99.4 (off)	0.005
<i>Colyidium nigripenne</i> LeConte	100 (off)	0.003
<i>Colyidium nigripenne</i> LeConte	25 (on)	0.031
<i>Corticiceus thoracicus</i> (Melsheimer)	99.9 (on)	0.001
<i>Cossonus</i> spp.	73.3 (off)	0.016
<i>Dendroctonus terebrans</i> (Olivier)	25 (on)	0.028
<i>Diplocoelus rufis</i> (LeConte)	36.4 (on)	0.021
<i>Gnathotrichus materiarius</i> (Fitch)	99.8 (on)	0.001
<i>Ips calligraphus</i> (Germar)	81.2 (on)	0.001
<i>Ips grandicollis</i> (Eichhoff)	37.5 (on)	0.003
<i>Lasconotus pusillus</i> LeConte	43.7 (on)	0.001
<i>Monochamus titillator</i> (Fabricius)	75 (on)	0.001
<i>Myoplatypus flavicornis</i> (Fabricius)	62.5 (on)	0.001
<i>Myrmecocephalus</i> sp.	46.3 (on)	0.001
<i>Nacaeus tenuis</i> (LeConte)	35.2 (on)	0.007
<i>Nitidulidae</i> sp. 9	43.7 (on)	0.002
<i>Orthotomicus caelatus</i> (Eichhoff)	55.8 (on)	0.001
<i>Platysoma cylindricum</i> (Paykull)	31.2 (on)	0.009
<i>Platysoma parallelum</i> (Say)	37.5 (on)	0.003
<i>Plegaderus transversus</i> (Say)	36.5 (on)	0.009
<i>Thoracophorus costalis</i> (Erichson)	82.1 (off)	0.031
<i>Xyleborus ferrugineus</i> (Fabricius)	52.7 (on)	0.001
<i>Xyleborus pubescens</i> Zimmermann	99.8 (on)	0.001
<b>Middle-aged log associates</b>		
<i>Cossonus</i> spp.	82.2 (on)	0.001
<b>Old log associates</b>		
<i>Conoplectus canaliculatus</i> (LeConte)	75 (off)	0.047
<i>Dioedus punctatus</i> LeConte	30.9 (on)	0.014
<i>Eblisia carolina</i> (Paykull)	93.3 (off)	0.012
<i>Palaminus</i> sp.	31.2 (on)	0.01
<i>Philothermus glabriculus</i> LeConte	80.4 (off)	0.043
<i>Staphylinidae</i> sp. 54	32.7 (on)	0.032
<i>Uloma punctulata</i> LeConte	88.6 (off)	0.016

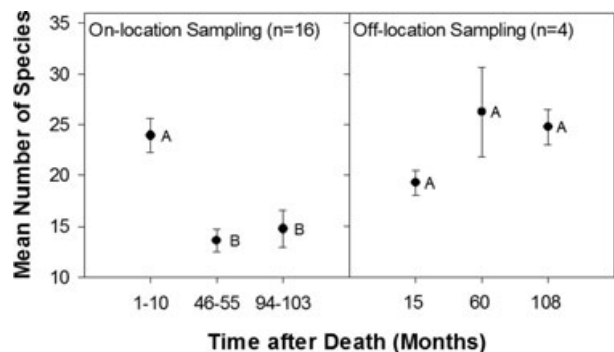
beetles, wood borers and predators), whereas those associated with old logs consisted of fungus-feeders and predators.

Significantly more species were collected from 1–10 month-old logs than from the older age classes in on-location sampling ( $F_{2,42} = 14.1$ ,  $P < 0.01$ ), although there were no differences in species richness among the three age classes sampled in off-location sampling ( $F_{2,9} = 1.7$ ,  $P = 0.2$ ) (Fig. 2).

### Discussion

Beetle species richness peaked within the first year (Fig. 2) as a result of the diverse community of bark beetles, wood-borers and predators associated with the phloem phase (Table 1). Although two observational studies on the succession of insects in Virginia pine in North Carolina and Maryland (Savely, 1939; Howden & Vogt, 1951) and research on black spruce in Canada





**Figure 2** Mean  $\pm$  SE number of beetle species collected from different aged loblolly pine logs using emergence traps on-location (i.e. in the field) and off-location (i.e. in the laboratory). Within each graph, means with different uppercase letters next to them are significantly different based on Tukey's Studentized range test. Note that the figure cannot be used to compare the efficiencies of the two trapping methods as a result of differences in sampling intensity.

(Saint-Germain *et al.*, 2007) support our conclusion that species richness declines after the phloem phase, research on *Populus* in Canada suggests the opposite is the case (Hammond *et al.*, 2004; Saint-Germain *et al.*, 2007). This discrepancy may be a result of differences between patterns of insect succession in conifers and angiosperms (Saint-Germain *et al.*, 2007). Research on other tree species would be of interest.

Although there were no significant differences in species richness among decay classes for off-location sampling, fewer species were collected on average from young logs than from the older age classes. The young logs were 15 months old when sampled off-location and were beyond the phloem phase, as demonstrated by the lack of phloem associates (Appendix 1). Species richness may increase for a period after the phloem phase as the wood becomes increasingly infiltrated by fungi and insects.

Because species composition differed among decay classes and a number of species were significantly associated with the oldest logs sampled in the present study, it is important to protect wood throughout the decomposition process in managed loblolly pine forests. The value of dead wood to conservation may be greatest at advanced stages of decay if, as discussed above, species associated with those stages are the most vulnerable as a result of poor dispersal powers. Although none of the species associated with old logs in the present study are known to be threatened or limited by poor dispersal abilities, it is important to note that there is a shortage of information regarding the status and dispersal abilities of most species in the southeastern U.S.A. Research on the relationship between dispersal ability and decay class association is needed.

Finally, patterns of beetle succession in loblolly pine snags (i.e. standing dead trees) are most likely different from the patterns observed in logs in this study. Beetle communities have been shown to differ in composition between loblolly pine snags and logs within the first year (Ulyshen & Hanula, 2009a), and probably exhibit dissimilar patterns or rates of succession. For example, Boulanger and Sirois (2007) found that beetle succession stopped in fire-killed black spruce snags after the phloem phase, and only continued after the snags fell to the

ground. Similar studies on succession in loblolly pine snags are needed to more fully understand the distribution and habitat requirements of saproxylic beetles.

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**Appendix 1** List of beetle species that emerged from loblolly pine logs off-location (i.e. in the laboratory) and on-location (i.e. in the field). The age of the logs, in months, is given at the top of each column

	Off-location			On-location			Total
	15	60	108	1-10	46-55	94-103	
<b>Aderidae</b>							
<i>Cnopus impressus</i> (LeConte)	0	2	16	1	0	1	20
<i>Ganascus ventricosus</i> (LeConte)	1	1	0	0	1	1	4
<i>Pseudariotus notatus</i> (LeConte)	0	1	0	0	0	0	1
<i>Aderidae</i> sp. 4	0	0	0	0	1	0	1
<b>Anobiidae</b>							
<i>Anobiidae</i> sp. 1	0	0	0	1	0	0	1
<b>Biphyllidae</b>							
<i>Diplocoelus rudis</i> (LeConte)	1	0	0	11	3	3	18
<b>Buprestidae</b>							
<i>Buprestis lineata</i> Fabricius	0	0	0	3	0	0	3
<i>Chalcophora virginiensis</i> Drury	0	5	1	0	1	2	9
<b>Carabidae</b>							
<i>Calathus opaculus</i> LeConte	0	0	0	1	0	0	1
<i>Clivina pallida</i> Say	0	1	0	0	0	0	1
<i>Coptodera aerata</i> Dejean	0	0	0	3	0	0	3
<i>Cyclotrachelus laevipennis</i> (LeConte)	0	0	0	0	1	1	2
<i>Cymindis limbatus</i> Dejean	0	0	0	0	1	0	1
<i>Dicaelus ambiguus</i> Laferte	0	0	0	1	0	1	2

## Appendix 1 Continued

	Off-location			On-location			Total
	15	60	108	1-10	46-55	94-103	
<i>Harpalus protractus</i> Casey	0	0	0	0	0	1	1
<i>Helluomorphoides</i> <i>clairvillei</i> (Dejean)	0	0	0	1	0	0	1
<i>Mioptachys flavicauda</i> Say	54	37	31	0	0	3	125
<i>Perigona nigriceps</i> Dejean	0	0	0	1	0	0	1
<i>Perigona pallipennis</i> (LeConte)	0	0	0	1	0	0	1
<i>Piesmus</i> <i>submarginatus</i> (Say)	0	0	0	2	14	10	26
<i>Polyderis laevis</i> Say	0	0	0	1	1	0	2
<i>Tachyta nana inornata</i> (Say)	3	3	1	1	1	1	10
Undetermined sp.	0	0	0	0	0	1	1
<b>Cerambycidae</b>							
<i>Acanthocinus</i> <i>nodosus</i> (Fabricius)	0	0	0	11	0	0	11
<i>Acanthocinus</i> <i>obsoletus</i> (Olivier)	0	0	0	89	0	0	89
<i>Monochamus titillator</i> (Fabricius)	0	0	0	41	0	0	41
<i>Xylotrechus sagittatus</i> (Germar)	1	0	0	1	0	0	2
<b>Cerylonidae</b>							
<i>Cerylon unicolor</i> (Ziegler)	0	0	0	5	0	0	5
<i>Philothermus</i> <i>glabriculus</i> LeConte	3	18	86	1	0	1	109
<b>Chrysomelidae</b>							
<i>Chrysomelidae</i> sp. 1	0	0	0	1	1	0	2
<i>Chrysomelidae</i> sp. 2	0	0	0	1	0	0	1
<b>Ciidae</b>							
<i>Ciidae</i> spp.	354	62	16	0	1	1	434
<b>Cleridae</b>							
<i>Priocera castanea</i> (Newman)	1	0	0	1	1	0	3
<i>Thanasimus dubius</i> (Fabricius)	0	0	0	1	0	0	1
<b>Coccinellidae</b>							
<i>Harmonia axyridis</i> (Pallas)	0	0	0	0	1	0	1
<b>Colydiidae</b>							
<i>Bitoma carinata</i> (LeConte)	0	0	0	1	0	0	1
<i>Bitoma quadriguttata</i> (Say)	0	0	0	0	3	0	3
<i>Colydium nigripenne</i> LeConte	37	0	0	17	0	0	54
<i>Lasconotus pusillus</i> LeConte	0	0	0	17	0	0	17
<i>Namunaria guttula</i> (LeConte)	1	0	0	2	0	0	3
<b>Corylophidae</b>							
<i>Corylophidae</i> spp.	1	1	0	0	2	0	4
<b>Cryptophagidae</b>							
<i>Cryptophagidae</i> sp. 2	0	0	0	3	3	0	6

## Appendix 1 Continued

<i>Cryptophagidae</i> sp. 3	0	0	0	0	1	0	1
<i>Cryptophagidae</i> sp. 4	0	2	0	10	3	3	18
<b>Curculionidae</b>							
<i>Cercopeus</i> sp.	0	0	0	0	0	1	1
<i>Cossonus</i> spp.	181	66	0	25	213	5	490
<i>Dendroctonus</i> <i>terebrans</i> (Olivier)	0	0	0	4	0	0	4
<i>Dryophthorus</i> <i>americanus</i> Bedel	10	40	1	0	5	1	57
<i>Gnathotrichus</i> <i>materiaris</i> (Fitch)	0	0	0	543	1	0	544
<i>Hylastes salebrosus</i> Eichhoff	0	0	0	3	0	0	3
<i>Hylastes tenuis</i> Eichhoff	0	0	0	0	0	1	1
<i>Ips avulsus</i> (Eichhoff)	0	0	0	1	0	1	2
<i>Ips calligraphus</i> (Germar)	0	0	0	89	0	0	89
<i>Ips grandicollis</i> (Eichhoff)	0	0	0	12	0	0	12
<i>Myoplatypus</i> <i>flavicornis</i> (Fabricius)	0	0	0	134	0	0	134
<i>Orthotomicus</i> <i>caelatus</i> (Eichhoff)	0	0	0	126	0	1	127
<i>Pityophthorus</i> spp.	0	0	0	0	0	1	1
<i>Rhyncolus</i> sp.	0	1	0	0	0	0	1
<i>Xyleborinus saxesini</i> (Ratzeburg)	0	0	0	1	0	2	3
<i>Xyleborus ferrugineus</i> (Fabricius)	10	0	0	30	1	1	42
<i>Xyleborus pubescens</i> Zimmermann	0	0	0	2525	0	4	2529
<i>Xylosandrus</i> <i>crassiusculus</i> (Motschulsky)	0	0	0	3	0	0	3
<b>Derodontidae</b>							
<i>Derodontus</i> <i>esotericus</i> Lawrence	0	0	0	0	3	0	3
<b>Elateridae</b>							
<i>Alaus myops</i> (Fabricius)	2	2	1	0	0	0	5
<i>Ampedus areolatus</i> (Say)	0	2	0	2	0	2	6
<i>Ampedus luteolus</i> LeConte	0	0	0	0	24	33	57
<i>Athous cucullatus</i> (Say)	0	0	0	3	7	3	13
<i>Dicrepidius ramicornis</i> (Palisot de Beauvois)	1	0	0	0	0	0	1
<i>Dipropus</i> spp.	1	2	4	1	2	12	22
<i>Drapetes</i> <i>quadripustulatus</i> Bonvouloir	1	0	0	0	2	0	3
<i>Lacon impressicollis</i> (Say)	0	2	0	1	0	0	3
<i>Megapenthes</i> <i>rufilabris</i> Germar	0	0	0	0	0	1	1
<i>Melanotus ignobilis</i> Melsheimer	0	1	3	98	1	1	104

## Appendix 1 Continued

	Off-location			On-location			Total
	15	60	108	1–10	46–55	94–103	
<i>Melanotus</i> sp. 2	0	0	0	1	0	2	3
<i>Neotrichophorus carolinensis</i> Schaeffer	0	0	0	2	0	1	3
<i>Orthostethus infuscatus</i> Germar	0	0	0	0	0	1	1
<b>Endomychidae</b>							
<i>Aphorista vittata</i> (Fabricius)	0	0	0	7	6	3	16
<i>Mycetina perpulchra</i> (Newman)	0	0	0	0	2	0	2
<i>Phymaphora pulchella</i> Newman	0	0	0	0	1	0	1
<b>Eucnemidae</b>							
<i>Dromaeolus</i> sp.	0	2	0	1	1	0	4
<i>Fornax</i> sp.	0	0	0	0	0	11	11
<b>Histeridae</b>							
<i>Aeletes floridae</i> (Marseul)	0	1	0	0	0	0	1
<i>Aeletes simplex</i> (LeConte)	0	0	0	1	0	0	1
<i>Bacanius punctiformis</i> (LeConte)	57	13	17	0	0	2	89
<i>Bacanius tantillus</i> LeConte	0	4	24	0	0	0	28
<i>Bacanius</i> sp. 3	0	0	3	0	0	0	3
<i>Caerosternus americanus</i> (LeConte)	0	0	2	0	0	0	2
<i>Eblisia carolina</i> (Paykull)	0	1	14	1	0	2	18
<i>Epiurus pulicarius</i> Erichson	2	8	7	0	0	0	17
<i>Paromalus seminulum</i> Erichson	0	1	17	0	0	2	20
<i>Platysoma cylindricum</i> (Paykull)	0	0	0	16	0	0	16
<i>Platysoma parallelum</i> (Say)	0	0	0	17	0	0	17
<i>Plegaderus barbelini</i> Marseul	0	0	0	1	0	0	1
<i>Plegaderus transversus</i> (Say)	0	0	0	38	1	0	39
<b>Hydrophilidae</b>							
<i>Hydrophilidae</i> sp. 1	0	0	0	1	0	1	2
<b>Laemophloeidae</b>							
<i>Cryptolestes</i> sp.	0	0	0	0	1	0	1
<i>Laemophloeus biguttatus</i> (Say)	0	0	0	1	0	0	1
<b>Lampyridae</b>							
<i>Lampyridae</i> sp. 1	0	0	0	1	0	0	1
<b>Latridiidae</b>							
<i>Latridiidae</i> spp.	0	0	0	4	10	4	18
<b>Leiodidae</b>							
<i>Agathidium</i> sp. 1	0	0	0	1	0	0	1
<i>Agathidium</i> sp. 2	0	1	5	2	0	2	10
<i>Anisotoma</i> sp.	0	0	0	0	0	2	2
<i>Ptomaphagus</i> sp.	0	0	0	1	0	0	1

## Appendix 1 Continued

<b>Lycidae</b>							
<i>Dictyopterus aurora</i> (Herbst)	0	0	0	0	0	1	1
<i>Plateros</i> spp.	0	25	12	0	24	15	76
<b>Micromalthidae</b>							
<i>Micromalthus debilis</i> LeConte	0	15	22	0	3	1	41
<b>Monotomidae</b>							
<i>Bactridium</i> sp.	0	0	0	2	0	0	2
<i>Monotoma</i> sp.	1	1	0	0	1	0	3
<i>Rhizophagus cylindricus</i> LeConte	0	0	0	2	0	0	2
<b>Mycetophagidae</b>							
<i>Litargus tetraspilotus</i> LeConte	0	0	0	1	1	0	2
<b>Nitidulidae</b>							
<i>Conotelus</i> sp.	0	0	0	1	0	0	1
<i>Palodes</i> sp.	0	0	0	0	1	0	1
<i>Thalycra</i> sp.	0	0	0	0	0	1	1
<i>Nitidulidae</i> sp. 7	0	0	0	2	2	1	5
<i>Nitidulidae</i> sp. 8	0	0	0	2	0	0	2
<i>Nitidulidae</i> sp. 9	0	0	0	12	0	0	12
<b>Passalidae</b>							
<i>Odontotaenius disjunctus</i> (Illiger)	0	0	0	0	2	1	3
<b>Passandridae</b>							
<i>Catogenus rufus</i> (Fabricius)	1	2	0	2	0	0	5
<b>Phalacridae</b>							
<i>Phalacridae</i> sp. 3	0	0	0	0	1	2	3
<i>Phalacridae</i> sp. 4	0	0	0	1	2	0	3
<b>Ptiliidae</b>							
<i>Ptiliidae</i> spp.	11	6	0	0	0	0	17
<b>Scarabaeidae</b>							
<i>Bolboceras thoracicornis</i> (Wallis)	0	0	0	0	0	1	1
<i>Euphoria sepulcralis</i> (Fabricius)	0	0	0	1	0	0	1
<b>Scraptiidae</b>							
<i>Canifa</i> sp.	0	0	1	0	0	0	1
<b>Scydmaenidae</b>							
<i>Scydmaenidae</i> spp.	1	21	20	1	7	8	58
<b>Silvanidae</b>							
<i>Ahasversus rectus</i> (LeConte)	0	0	0	3	1	1	5
<i>Cathartosilvanus imbellis</i> (LeConte)	0	0	0	1	0	1	2
<i>Silvanus muticus</i> Sharp	0	0	0	11	5	3	19
<i>Uleiota dubius</i> (Fabricius)	1	0	0	0	0	0	1
<b>Sphindidae</b>							
<i>Sphindus</i> sp.	0	3	8	0	0	5	16
<b>Staphylinidae</b>							
<i>Acrolocha</i> sp.	0	0	0	2	10	1	13
<i>Actiastes</i> sp.	0	0	14	0	0	0	14
<i>Anacyptus testaceus</i> (LeConte)	3	3	2	0	0	0	8
<i>Batriasymmodes</i> sp.	1	0	0	0	1	1	3
<i>Batrisodes unicolornis</i> (Casey)	0	0	0	0	0	3	3

## Appendix 1 Continued

	Off-location			On-location			Total
	15	60	108	1–10	46–55	94–103	
<i>Clavilispinus</i> sp.	1731	10	0	1	55	4	1801
<i>Conoplectus</i> <i>canaliculatus</i> (LeConte)	0	0	27	0	0	0	27
<i>Coproporus</i> <i>ventriculus</i> (Say)	78	2	48	1	2	3	134
<i>Dalmosanus</i> sp.	0	0	1	0	0	0	1
<i>Echiaster</i> sp.	0	0	0	2	3	1	6
<i>Euplectus duryi</i> Casey	0	0	10	0	0	0	10
<i>Euplectus</i> sp. (female)	0	3	23	0	0	0	26
<i>Gyrophypnus</i> sp.	3	6	1	3	1	4	18
<i>Hesperus</i> sp.	0	0	0	0	0	1	1
<i>Laetulonthus laetulus</i> (Say)	0	0	0	1	0	0	1
<i>Leptoplectus</i> <i>pertenuis</i> (Casey)	0	0	0	0	1	3	4
<i>Lordithon angularis</i> (Sachse)	0	0	1	0	0	0	1
<i>Lordithon obsoletus</i> (Say)	0	0	0	0	0	1	1
<i>Megalopinus caelatus</i> (Gravenhorst)	0	0	0	0	0	1	1
<i>Melba</i> sp. (female)	0	1	0	0	0	0	1
<i>Melba parvula</i> (LeConte)	4	1	0	0	0	0	5
<i>Melba sulcatula</i> Casey	0	0	24	0	0	0	24
<i>Myrmecocephalus</i> sp.	0	0	0	14	2	1	17
<i>Nacaeus tenuis</i> (LeConte)	0	0	0	15	0	1	16
<i>Oxyporus femoralis</i> <i>austrinus</i> Horn	0	0	0	0	1	0	1
<i>Palaminus</i> sp.	0	0	2	2	1	15	20
<i>Proteinus</i> sp.	0	0	0	0	0	1	1
<i>Pycnoplectus</i> sp. (female)	0	1	0	0	0	0	1
<i>Pycnoplectus</i> <i>interruptus</i> (LeConte)	0	10	4	1	2	2	19
<i>Pycnoplectus linearis</i> (LeConte)	0	0	0	0	3	1	4
<i>Pycnoplectus sexualis</i> (Casey)	0	0	0	2	1	1	4
<i>Scaphidiinae</i> sp. 2	0	0	0	0	1	1	2
<i>Scaphidiinae</i> sp. 3	3	1	35	1	0	2	42
<i>Scaphidium</i> sp.	0	0	0	0	0	1	1
<i>Sepedophilus scriptus</i> (Horn)	0	0	152	0	5	10	167
<i>Sepedophilus</i> sp. 2	0	0	4	5	11	20	40
<i>Sepedophilus</i> sp. 3	0	0	2	0	5	8	15
<i>Sepedophilus</i> sp. 4	0	0	0	8	13	10	31
<i>Stilicopsis</i> sp.	0	0	0	0	1	0	1
<i>Thesiastes pumilis</i> (LeConte)	0	0	0	0	1	0	1
<i>Thinocharis</i> sp.	0	0	0	4	0	0	4
<i>Thoracophorus</i> <i>costalis</i> (Erichson)	23	5	0	0	0	2	30
<i>Tmesiphorus costalis</i> LeConte	0	7	14	0	1	0	22

## Appendix 1 Continued

<i>Tyrus consimilis</i>	1	1	0	0	3	1	6
Casey							
<i>Staphylinidae</i> sp. 29	0	0	7	11	1	27	46
<i>Staphylinidae</i> sp. 50	0	0	2	0	0	0	2
<i>Staphylinidae</i> sp. 51	0	0	0	1	0	0	1
<i>Staphylinidae</i> sp. 52	0	0	0	0	1	0	1
<i>Staphylinidae</i> sp. 53	0	1	9	0	0	0	10
<i>Staphylinidae</i> sp. 54	0	4	0	5	4	17	30
<i>Staphylinidae</i> sp. 55	0	1	0	0	0	0	1
<i>Staphylinidae</i> sp. 56	0	0	0	0	0	1	1
<i>Staphylinidae</i> sp. 57	1	0	0	11	1	3	16
<i>Staphylinidae</i> sp. 58	0	1	4	19	13	15	52
<i>Staphylinidae</i> sp. 59	0	0	1	0	0	0	1
<i>Staphylinidae</i> sp. 60	0	0	0	0	0	1	1
<i>Staphylinidae</i> sp. 61	1	0	0	0	0	0	1
<i>Staphylinidae</i> sp. 62	0	0	0	0	2	1	3
<i>Staphylinidae</i> sp. 63	0	0	0	1	0	0	1
<i>Staphylinidae</i> sp. 64	2	1	0	0	0	0	3
<i>Staphylinidae</i> sp. 65	0	0	1	0	0	2	3
<i>Staphylinidae</i> sp. 66	0	0	0	1	1	5	7
<b>Tenebrionidae</b>							
<i>Corticeus parallelus</i> (Melsheimer)	0	0	0	1	0	0	1
<i>Corticeus thoracicus</i> (Melsheimer)	0	0	0	914	0	1	915
<i>Dioedus punctatus</i> LeConte	0	13	69	0	1	91	174
<i>Helops cisteloides</i> Germer	0	0	0	1	2	0	3
<i>Hymenorus</i> sp.	0	0	30	4	3	5	42
<i>Lobopoda</i> <i>erythrocnemis</i> Germer	0	0	5	0	0	1	6
<i>Platydema flavipes</i> (Fabricius)	0	1	0	1	1	1	4
<i>Platydema ruficorne</i> (Stürm)	0	0	0	1	0	0	1
<i>Poecilocrypticus</i> <i>formicophilus</i> Gebien	0	1	0	0	0	0	1
<i>Uloma punctulata</i> LeConte	4	29	256	0	18	78	385
<b>Tetratomidae</b>							
<i>Eustrophopsis bicolor</i> (Fabricius)	0	0	0	1	0	0	1
<i>Holostrophus</i> <i>bifasciatus</i> (Say)	0	0	0	0	1	1	2
<b>Throscidae</b>							
<i>Aulonothroscus</i> <i>convergens</i> (Horn)	0	0	27	62	21	31	141
<i>Aulonothroscus</i> sp.	1	0	0	1	2	1	5
<b>Zopheridae</b>							
<i>Hyporhagus</i> <i>punctulatus</i> Thomson	0	0	0	6	0	0	6
<i>Pycnomerus</i> <i>haematodes</i> (Fabricius)	20	37	0	4	3	1	65
<i>Pycnomerus</i> <i>sulcicollis</i> LeConte	19	23	21	18	14	15	110
Total individuals (species)	2632 (41)	516 (58)	1108 (52)	5094 (112)	584 (86)	572 (102)	10 506 (209)

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