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Succession of Coleoptera on freshly killed loblolly pine (Pinus taeda L.) and southern red oak (Quercus falcata Michaux) in Louisiana

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SUCCESSION OF COLEOPTERA ON FRESHLY KILLED LOBLOLLY PINE (*PINUS TAEDA* L.) AND SOUTHERN RED OAK (*QUERCUS FALCATA* MICHAUX) IN LOUISIANA

A Thesis

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DEDICATION

This thesis is dedicated to my parents who have sacrificed all to give me and my siblings a proper education. I am indebted to my entire family for the moral support and prayers throughout my years of education. My mother and Aunt Gloria will have several extra free hours a week now that I am graduating. I owe so much to my twin sister Stacey, the cheerleader of my life. Motivation provided by Ignacio was the constant factor helping me to move forward.

I also dedicate this work to all my fellow New Orleanians who suffered through that great American tragedy called Hurricane Katrina. While attending LSU, Baton Rouge has been my mailing address, but New Orleans is my home. For the survivors it has taken years to rebuild our lives but rebuilding the city will take even longer. Toil and sweat are temporary; we will achieve greatness once again. Soon we will have the heart to exclaim, "Laissez les bon temps rouler!"

⚜

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ABSTRACT

Wood is important in forest ecology because its large biomass serves as a nutritional substrate and habitat for many organisms, including Coleoptera, and beetles contribute greatly to nutrient recycling in forests. Overlapping complexes of beetles invade dead wood according to the species of tree, ambient conditions, and most importantly, stage of decomposition. Beetle succession was studied in loblolly pines (*Pinus taeda* L.) and southern red oaks (*Quercus falcata* Michx.) by documenting beetle arrival and residency in cut, reassembled, and standing bolts. Twelve trees of each species at Feliciana Preserve in West Feliciana parish, LA were felled during October 2004 and April 2005 for a total of 24 trees sampled from October 2004 – September 2005. Four 48-inch bolts were cut from each felled tree. Each bolt was further cut into eight six-inch sections, reassembled in proper order, and positioned standing upright. Beetles were aspirated from section interfaces weekly the first month and then monthly for the duration of the study.

A total 51,119 specimens from 190 taxa were collected from 3822 samples during 18 sampling events. Species richness and abundance were higher on southern red oak wood (144 taxa, 40874 specimens) than loblolly pine (122 taxa, 10245 specimens); abundance was significantly higher. Colonization and species composition patterns of coleoptera were significantly affected by host tree species, the season in which the tree died, the period of decay, the position or height along the woody substrate and many complex interactions of these effects. Loblolly pine bolts showed a slightly more rapid turnover of taxa than southern red oak bolts. Wood characteristics such as loss of moisture, which caused bark to loosen on pines, and higher quality substrate hardwood in oaks presumably account for the greater number of taxa and specimens collected from southern red oak than loblolly pine. This study has increased the

number of species known to inhabit recently dead loblolly pine and southern red oak, two economically important tree species. Studies of this nature supplement investigations into the importance of coarse woody debris in forests by documenting ecological patterns of saproxylic coleoptera.

CHAPTER 1: INTRODUCTION

Forests are arenas where trees and their inhabitants interact. Environmental benefits of forests include water flow control, soil conservation, and atmospheric uptake of CO_2. Trees convert CO_2 into complex carbohydrates via photosynthesis, release O_2 into the air, and provide shelter and nutrients for innumerable organisms, particularly insects. Fallen logs, limbs, twigs and standing snags make up the physical components that a forest requires for a healthy ecosystem. These components are referred to as coarse woody debris (CWD) and are key substrates for forest biodiversity. Protection and conservation of forests and their inhabitants are important responsibilities practiced by forest managers and silviculturists, and maintaining biodiversity is a crucial element in this discipline.

Forest management takes on an added dimension when human needs are involved. The inherent properties of wood have always made it attractive as a resource for fuel, building material, furniture, textile fibers, and paper products. Forest managers strive to maintain balance in forest ecosystems while acknowledging our necessity for wood products (Gladstone and Ledig 1990). Almost all old growth forests in eastern North America were disturbed or harvested during the past two centuries. Awareness of the dire consequences by the end of the 19th century led the United States government to implement laws to protect old growth forests and explore the potential of sustainable forests. By 1905 the Transfer Act was passed. The United State Department of Agriculture's new Bureau of Forestry, commonly known today as the US Forest Service, began management of 85,627,472 acres of forest reserves (Conners 2007). In the last century, renewable forests for harvest, timber plantations, were established to provide a sustainable source of timber products. Timber plantations now constitute nearly five percent of the world's four billion hectares of forests (FAO 2000). Renewable forests are commonly high yield, low diversity, often monoculture forests. A vast increase in woodlands meant an increase in resources to the myriad of organisms that use them for shelter, reproduction, and food supply. At its inception Investigations into the "pest" status of resident insects soon were undertaken. Forest entomology in the United States began during the late 1880s with notable leaders A. D. Hopkins, the father of American forest entomology, and Asa Fitch (Edmonds *et al*. 2000). Forest entomology is a field of science that aims to identify insect pests of trees, investigate tree stresses, monitor tree health, and integrate management strategies. Entomology research has provided better knowledge about ways to improve forest conditions for wildlife inhabitants and sustainable sources of timber by documenting the complex interactions between insects and trees.

As dead trees decay, an overlapping succession of insects invades according to the condition of the tree (Howden and Vogt 1951). Succession is defined as the continual replacement of species within a particular area over time (Gutierrez and Fey 1980). Studying succession allows detection of historical patterns of distributions among organisms as well as future forecasts of species in similar settings. Patterns of insect succession in decaying wood vary according to moisture content, weather, temperature, and tree species (Howden and Vogt 1951; Harmon *et al.* 1986; Zhong and Schowalter 1989). The community of saproxylic insects – those that depend on dead wood or other dead wood-dependent organisms at some point during the life cycle (Speight 1989) – in wood of advanced decay is composed mostly of saprovores feeding on fungi and microbial substrates that eventually overwhelm and consume dead wood (Howden and Vogt 1951).

Coleoptera are the most diverse order of insects that utilize trees. Multiple functional groups of beetles, including predators, fungivores, and detritivores, aid in breaking down nutrients locked within dead or dying limbs and snags and on the forest floor (Zhong and Schowalter 1989). Beetle families Curculionidae, Buprestidae, and Cerambycidae typically initiate attacks (Harmon *et al*. 1986; Zhong and Schowalter 1989; Savely 1939). They can infest and damage living trees but especially thrive on stressed or freshly killed trees. Freshly killed trees release volatiles (*e.g.,* α – pinene found in pine resin) that attract flying beetles and other insects (Renwick and Vité 1969; Raffa and Berryman 1983; Borden *et al*. 1987). Decomposition of recently dead wood or stressed trees of many species is accelerated by aggregating bark beetles (Curculionidae: Scolytinae) that release pheromones to attract large numbers of conspecifics (Ferrell 1971) and double as allomones that attract predators and parasites (Camors and Payne 1972). Decomposition is also enhanced by beetles because they provide entry points into the wood and introduce "mutualistic microflora" (Zhong and Schowalter 1989).

Previous studies detailing succession of decayed wood dates back to 1916 with Shelford's study of fallen tree trunks and standing dead trees. Graham (1925) examined the primary colonizers of conifers with special emphasis on the effects of temperature and moisture content. Blackman and Stage (1924) sampled insects from dead and dying hickory trees for five years in order to examine the insects' succession patterns. A definitive succession study by Savely (1939) detailed environmental factors and their effects on insects' colonization of decaying pine and oak logs. Howden and Vogt (1951) sampled Virginia Pine snags weekly for one year. Hines and Heikkenen (1977) studied succession of beetles on dead Virginia Pine by severing dead trees **monthly** from April – September and sampling weekly for eight months.

Some previous succession studies were conducted on decaying standing trees (Shelford 1913; Blackman and Stage 1924), entire standing, severed trees (Hines and Heikkenen 1977; Ferrell 1971; Howden and Vogt 1951; Gaumer and Gara 1967), or on logs – bolts – cut from the tree and oriented horizontally, slightly above the ground (Riley 1983). Studies done on standing severed trees used passive and pheromone traps to assess which species were present (Hines and Heikkenen 1977, Ferrell 1971). This method is certainly useful, but indirect methods of detection and collection may be inaccurate (Cronin *et al*. 2000). Cronin *et al.* (2000) used powder pigment applied to the bark of a southern pine beetle infested tree in an attempt to track beetles that were in contact with the tree and found no correlation between emerged adults and trap collected individuals. Traps used included passive sticky traps, multi-funnel traps, and pine trees baited with attractants. Traps can be useful for pest management surveys but a true succession study requires a more direct approach.

The recognition that beetle succession on freshly killed CWD is rapid and often complex prompted the study that is the topic of this thesis. The initial impetus for conducting this study using cut sections of a felled tree base was based on the results of a unique collection method for beetles conceived by the late coleopterist Karl Stephan. He felled a living tree and cut it into stackable disks which could be examined for beetles at any desired frequency during a long period of time (Stephan 1989; Carlton *et al*. 2005). In Europe, different techniques are employed, but Abrahamsson and Lindbladh (2006) looked at man-made snags (3-5 m high) in Sweden to examine beetle occurrence on spruce. I used a standardization of Stephan's collection method to study beetle succession on felled loblolly pines (*Pinus taeda* L.) and southern red oaks (*Quercus falcata* Michaux) by documenting beetle arrival and residency. Hines and Heikkenen (1977) found the greatest differences in saproxylic beetle abundances from Virginia pines severed in April and September. Based on this finding, trees were felled in this study during early fall (October 2, 2004) and mid-spring (April 2, 2005). This study took place in Louisiana where loblolly pines and southern red oaks are of great economic importance. The Feliciana

Preserve provided the area of research for this study and is located in the Tunica Hills area north of Baton Rouge. A more detailed description of this locality is provided in the description of habitat section of the Materials and Methods.

1.1 Justification

This work documents novel information about saproxylic beetles and their succession patterns and distribution in a south Louisiana mixed mesophytic forest. Loblolly pine was selected because it is a dominant tree in many southern forests, it is the preferred host of many beetle species (Thatcher *et al.* 1980), and it is an important timber species for the wood industry. Southern red oak was selected to represent deciduous tree species because it is a dominant deciduous species and deciduous trees have not usually been included in previous studies of this type.

Wood is important in forest ecology because its large biomass serves as a nutritional substrate for Coleoptera, and beetles contribute greatly to nutrient recycling in forests. Forest management practices such as dead wood retention are vital to enhancing beetle diversity. Kaila *et al*. (1997) found that "management measures matching suppressed natural disturbances [were] found useful in preserving diversity in managed forests." As forest areas shrink some saproxylic insects will not survive and will become regionally extinct. Understanding the succession of insect complexes that inhabit a freshly killed tree may help prevent such regional extinctions by optimizing management practices that preserve beetle diversity. Before the roles of beetles in the sustainability of forest productivity could be understood, we must first study the basic ecological interactions of beetle species or assemblages of species colonizing different tree types through time and space.

1.2 Research Objectives

The general purpose of this research project was to document beetle succession of felled loblolly pines and southern red oaks by determining which species of beetles colonize freshly killed standing tree bolts and the sequence of each species' arrival.

The specific objectives were:

OBJECTIVE 1. To compare beetle species present on freshly severed bolts of two tree species. It was expected that large abundances of a few scolytines and other saproxylic species would colonize and overpower defenses of loblolly pine (Coulson 1979; Raffa *et al.* 1993) while multiple species would be attracted to southern red oak wood and the expected immediate colonization of fungi.

Hypothesis: Beetle species composition patterns should differ between loblolly pines and southern red oak bolts. Loblolly pine bolts should show a higher abundance of specimens collected, whereas southern red oak bolts should show higher species richness.

OBJECTIVE 2. To record the arrival sequence of beetle species that inhabit felled and cut loblolly pine and southern red oak trees reassembled into standing bolts. It was expected that different species' host specificities, based on the differences in wood characteristics, would affect the way in which saproxylic coleoptera colonize freshly killed bolts of loblolly pine and southern red oak (Harmon *et al.* 1986; Hanula 1996).

Hypotheses: Beetle species succession patterns will differ between loblolly pine and southern red oak bolts. Loblolly pine bolts will show a more rapid turnover of beetle taxa, whereas southern red oak bolts will show a more gradual turnover.

OBJECTIVE 3. To compare beetle species succession on standing bolts between early fall and mid-spring treatment dates. It was expected that climatic conditions associated with each season would affect the way in which saproxylic coleoptera colonize bolts of freshly killed trees as seen in a previous study (Hines and Heikkenen 1977).

Hypothesis: Beetle species succession patterns should differ between trees felled in early fall and trees felled in mid-spring.

CHAPTER 2: MATERIALS AND METHODS

2.1 Description of Habitat

The locality of this study is the Feliciana Preserve in West Feliciana Parish, Louisiana, located 56.3 km north of Baton Rouge and 16.1 km east of St. Francisville (30° 47’ N, 91° 15’ W) (Figure 2.1). Feliciana Preserve consists of 60.7 ha of undeveloped, privately owned land. It was selectively logged 39 years ago (Landau *et al*. 1999) in 1969. Feliciana Preserve is bordered by Hammer Creek on the northwest and Thompson Creek on the southeast (Figure 2.2). Upland sites in West Feliciana have a mixed mesophytic hardwood association with magnolia (*Magnolia grandifolia* L.), American holly (*Ilex opaca* Aiton), and beech (*Fagus grandifolia* Ehrhart) (Delcourt and Delcourt 1974). Other tree species found at Feliciana Preserve are yellow poplar (*Liriodendron tulipifera* L.), loblolly pine, various oaks such as water oak (*Quercus nigra* L.) and southern red oak. The understory is a mixture of small trees, shrubs, and vines. This mixed mesophytic hardwood forest is in middle succession, transitioning between large, old pines (a pine-oak secondary forest) and near complete deciduous floral composition (magnolia, beech, and oak).

Figure 2.1. Location of the Feliciana Preserve (star) in West Feliciana Parish, LA.

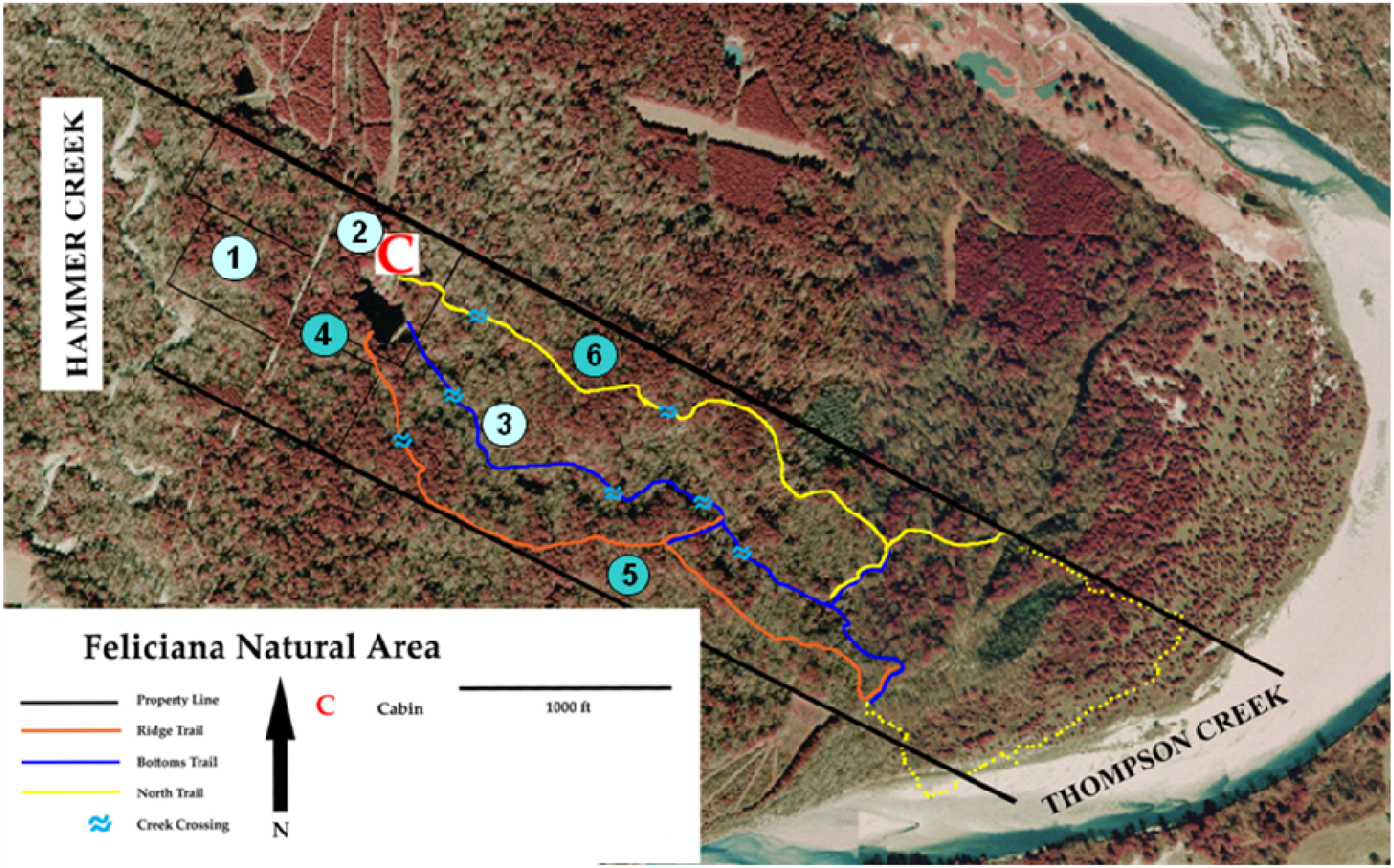


Figure 2.2. Aerial photo of Feliciana Preserve showing the layout of six study sites. Sites 1, 2, and 3 were used during season 1 while sites 4, 5, and 6 were used during season 2.

Feliciana Preserve is located about 50 km east of the Tunica Hills (Landau *et al.* 1999), which is known to occupy the southernmost distribution of mixed mesophytic forest in an area known as the Blufflands (Delcourt and Delcourt 1975). The Blufflands is “a belt of hilly land bordering the eastern escarpment of the Mississippi River alluvial valley” (Delcourt and Delcourt 1975) stretching from Tennessee and Mississippi to Louisiana. The forest type extends south past its usual Appalachian Mountains range as a result of climatic conditions present during the last continental glaciations of the Pleistocene. Streams and the flow of the Mississippi River contribute to the characteristic ravines cut into the Blufflands belt. The soils and cool, moist climate lingering in the ravines help to retain mixed mesophytic hardwood forest this far south. Consequently, Blufflands habitats host a number of disjunct flora and fauna with northern distributions (Delcourt and Delcourt 1975), making it an interesting area biogeographically.

2.2 Study Sites

Six sites were chosen throughout Feliciana Preserve (Figure 2.2). Sites were separated an average distance of 254 meters from the two closest neighboring sites. No other tree removal study was conducted during the time of this study. The study area was generally homogeneous with regard to soil quality, canopy cover, leaf litter, amount of dead wood in the surrounding area, land drainage, *lack* of pesticide use, and lack of artificial lighting. Site 1 (elevation 39.6 m) was located near the west property line along Hammer Creek and was located about 0.8 km from a road. Site 2 (elevation 41.1 m) was near a ravine in an area with a mostly open canopy. Site 3 (elevation 33.5 m) was next to the Bottoms (blue) trail in the central area of the Preserve. Site 4 (elevation 41.1 m) was located near a man-made pond. Site 5 (elevation 33.5 m) was situated south of the point at which the Ridge (orange) and Bottoms (blue) trails first run conjointly. Site 6 (elevation 42.7 m) was positioned along the North (yellow) trail.

2.3 Experimental Design

The experiments were setup during two seasons, modeled after the two greatest felling month differences in saproxylic beetle abundance recorded by Hines and Heikkenen (1977). They found the greatest difference between comparisons of trees felled during April and September. To equally space the tree fellings, October and, exactly six months later, April were chosen. Twelve trees were felled on October 2, 2004 (start of season 1) and 12 on April 2, 2005 (start of season 2). The sampling regimen continued through September 2005. Season 1 samples were collected at sites 1-3 while season 2 was conducted at sites 4-6. Diameter at breast height (DBH) and approximate age were recorded for all trees (Table 2.1). DBH is a standard measure of a tree's diameter and is taken at 4.5 feet (~1.3 m) above the ground. Ring counts were used to approximate age (Avery 1975). Two trees each of loblolly pine and southern red oak were felled at each site. The four trees were located at least ten meters away from one another.

To increase 'replicates,' the lowest 16 feet (4.88 m) of each tree was subdivided into four bolts. Bolts were marked with the letter designations A-D to denote their position within the tree. Bolt A was the piece cut above the roots. B was the bolt cut above A, and so on (Figure 2.3). The 48-inch (1.22 m) bolts were then cut into eight 6-inch (15.24 cm) sections, and the sections were reassembled in proper order, and placed vertically on the ground to emulate short snags. The lowest section acted as the base or pseudo-stump. Above the base, the sections were numbered 1-7, with the highest section only serving as a cap to provide the top half of the sixth interface. Metal flashing triangles were affixed to each section with the point facing the interface. Nail heads on the next section were used to make a visual straight line along the length of the bolt to correctly align the sections when sampled (Figure 2.4). The upright bolt assemblies were stacked on the ground approximately five meters apart. Bolts A-C were used to collect samples from section interfaces while bolt D was used to collect samples from beneath the bark (Figure 2.3). A total of 96 bolts (72 - section interface study, 24 - bark removal study) were erected for the entire project (three sites/season, four trees/site, four bolts/tree).

2.4 Sampling

A total of 15 sampling events were completed during season 1. The first nine events

Table 2.1. Diameter at breast height (DBH) and approximate age for sites 1-6 during Season 1 (October 2004-September 2005) and Season 2 (April-September 2005) (N=24).

Season	Site	Tree	Age (years)	DBH (cm)
1	1	Pine 1	42	29.97
1	1	Pine 2	37	27.18
1	1	Oak 1	45	31.24
1	1	Oak 2	45	26.16
1	2	Pine 1	45	34.04
1	2	Pine 2	40	31.24
1	2	Oak 1	39	30.23
1	2	Oak 2	39	23.37
1	3	Pine 1	37	28.19
1	3	Pine 2	52	36.07
1	3	Oak 1	37	28.19
1	3	Oak 2	50	29.21
2	4	Pine 1	25	33.53
2	4	Pine 2	25	32.00
2	4	Oak 1	35	32.77
2	4	Oak 2	39	28.70
2	5	Pine 1	48	26.67
2	5	Pine 2	48	27.69
2	5	Oak 1	47	25.15
2	5	Oak 2	50	29.72
2	6	Pine 1	35	31.75
2	6	Pine 2	50	33.02
2	6	Oak 1	53	26.92
2	6	Oak 2	42	28.19

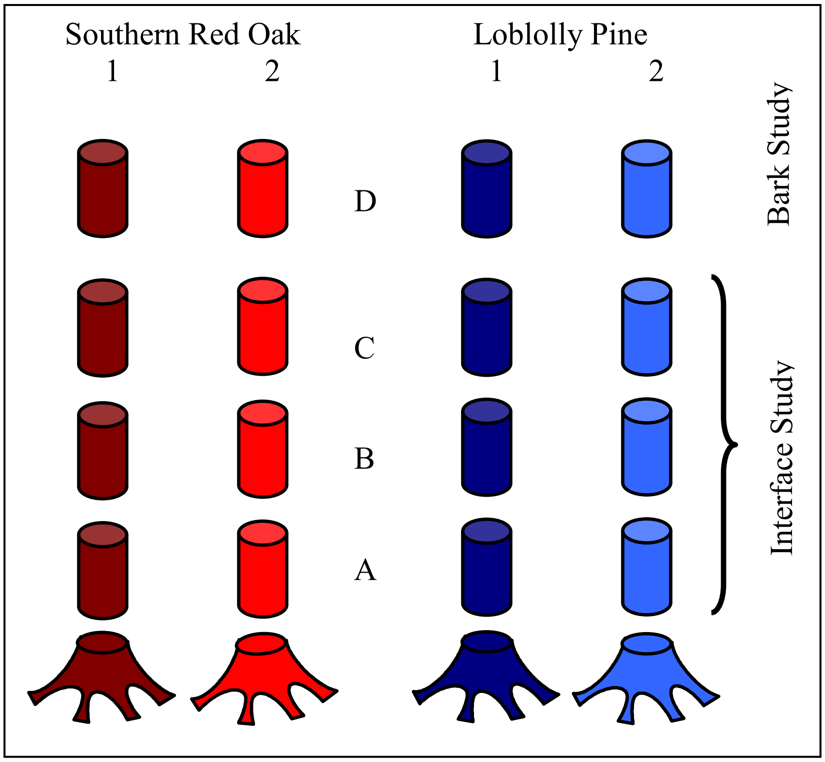


Figure 2.3. Diagram of a site showing the usage of bolts. Two southern red oak and loblolly pine trees were felled per site and the lowest 16' of the bole above the roots was divided into four bolts used to sample insects from section interfaces and beneath bark.

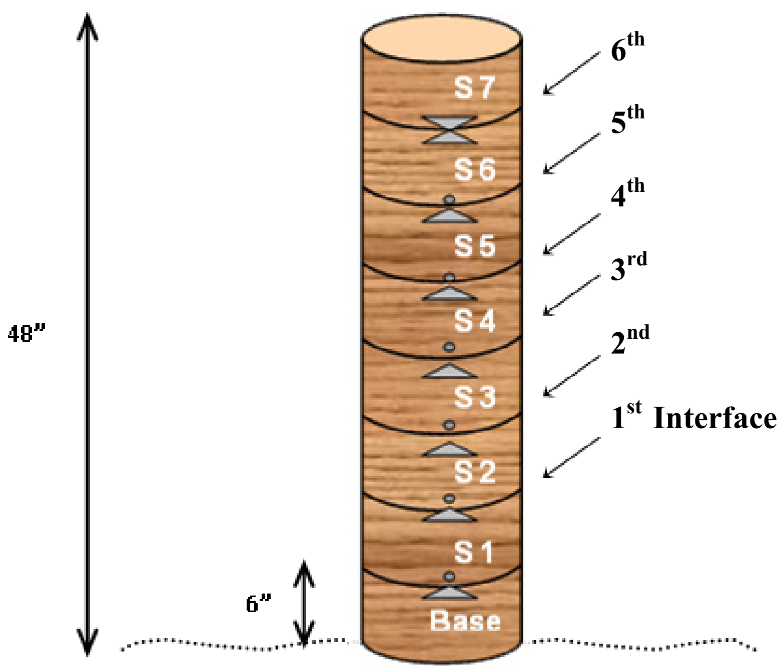


Figure 2.4. Division of a 4' bolt into 6" sections. Samples were collected from the interfaces.

Table 2.2. Temperature and relative humidity for 18 sampling events during Season 1 (in part, October 2004-March 2005) and Season 2 (April-September 2005). All measurements were recorded at noon (+/- 30 minutes).

Season	Date	Temperature (°F)	Relative Humidity (%)
1	11-Oct-04	78.5	71.5
1	18-Oct-04	81.6	70.0
1	25-Oct-04	81.0	72.0
1	1-Nov-04	80.9	63.0
1	29-Nov-04	72.0	66.0
1	27-Dec-04	65.2	37.5
1	24-Jan-05	45.0	43.5
1	21-Feb-05	79.0	64.5
1	21-Mar-05	74.2	64.0
2	11-Apr-05	73.6	76.0
2	18-Apr-05	73.9	38.0
2	4/25/2005 *	61.6	70.0
2	2-May-05	73.0	41.0
2	5/30/2005 *	77.6	92.0
2	27-Jun-05	87.1	57.0
2	25-Jul-05	91.9	59.0
2	22-Aug-05	89.1	64.0
2	19-Sep-05 **	87.0	85.0

* Dates with above average rainfall.
** Sampling event occurred after Hurricane Katrina struck near New Orleans, LA August 29, 2005.

(October 2004 – March 2005) were processed and included in data analyses. Nine sampling events were completed during season 2 and all were processed and analyzed. Temperature (°F), relative humidity (%), and major weather events were recorded at noon (+/- 30 minutes) for each sampling event (Table 2.2). After felling, samples were collected once a week during the first month and monthly thereafter for an additional 11 months (season 1) or five months (season 2). Given that only the first nine sampling events of season 1 were processed, a total six month sampling period for each season was analyzed. Working from interface six down to one, insects were mechanically "aspirated" with cordless, handheld vacuums (Bug Catcher Vacuum; Insect Aside, Farmington, WA), slightly customized, or hand collected with forceps into vials containing 75% ethyl alcohol. Samples were collected from section interfaces and beneath bark. After each bolt was sampled, the sections were vertically re-stacked in correct order and kept in alignment using the metal flashing triangles and nail heads.

2.4.1 Section Interfaces

A separate vial was used for each of the six interfaces of bolts A, B, and C during the section interface study. For each sampling event, 216 samples (*i.e.,* vials) were collected. Wind and/or imbalance tipped over ten bolts during season 1 and one bolt from season 2. The bolts were repositioned vertically at first opportunity. Despite blown down trees and branches, surprisingly, no bolts tipped over after Hurricane Katrina struck on August 29, 2005. These 66 samples represent missing data, not zeros, and therefore were not included in the data set. A grand total of 5,118 samples were collected throughout the section interface study. Of this total **3,822** samples from 18 sampling events were included in data analyses.

2.4.2 Bark Removal

Destructive sampling was used in addition to section interface inspection to investigate species colonizing beneath bark. A simple screwdriver and hammer facilitated bark removal from sections. The sampling regimen was determined by dividing the number of months spanning each season – 12 and six for season 1 and 2, respectively – by the six sections in bolt D. Consequently, beetles were sampled every two months for season 1 and monthly for season 2 in 12 total bark removal sampling events. One section's bark was examined per sampling event, starting with section six. Insects from the interface above the sampled bark section were also collected, in a separate vial, for added reference. Bark removal study samples (*i.e.,* vials) numbered 288 for both seasons; 144 subcortical samples and 144 from interfaces. No bark removal samples were used for taxa checklists nor analyses due to low sample yields comprised mostly of larvae versus adults. Samples were archivally preserved for possible future analysis.

2.5 Sample Analysis

Samples were sorted, representative specimens mounted, and residues preserved in 75% ethyl alcohol. Only specimens of adult Coleoptera were used for analyses. Insect specimens of all other orders and Coleoptera larvae were archivally preserved in 75% ethyl alcohol for future study. Beetles were identified to species or sorted to morphospecies when species determinations were not feasible. Species were identified using taxonomic keys available from *American Beetles* (Arnett and Thomas 2001; Arnett *et al*. 2002), species-level revisions cited therein, and other primary literature. Species identifications were verified by comparison to authoritatively identified specimens from the Louisiana State Arthropod Museum (LSAM). Specimen and species numbers were recorded for statistical analyses. A collection of voucher specimens was deposited in the LSAM, Louisiana State University, Baton Rouge.

2.6 Data Analysis

Of the 190 species level taxa identified, the 30 most abundant were used for most statistical analyses. These 30 taxa, "reduced dataset", represented 96.5 % of all specimens (Appendixes B, C). A standard practice of using only those species representing a minimum of five percent each of the total specimens was impractical for my goal of detecting patterns in species assemblages given that only four species would have met the criterion. Independent variables included in the dataset were season of tree felling, decay week (*i.e.,* number of weeks since trees were felled), site, tree species, tree replicate, bolt, section (*i.e.,* the interface sampled), beetle species and their abundance. For some analyses, species counts were log (x+1) transformed to lessen their non-normal distributions. Diameter at breast height and age were compared with analyses of variance among all 24 trees to establish that sample trees were uniform.

Consultation with Dr. Barry Moser (deceased) and Dr. James Geaghan of Louisiana State University's Department of Experimental Statistics guided the project's experimental design and statistical analyses. The analyses were performed using SAS/STAT® software, Version 9.1.3 of the SAS System (SAS Institute 2004) for Microsoft® Windows®. All analyses were performed with the confidence level α set at 0.05.

Frequency information was analyzed using the FREQ procedure to determine the association of beetles on loblolly pine and southern red oak as well as the abundance of specimens and species richness (**Objective 1**). Beetle species composition overall was evaluated by a MANOVA (Proc GLM) test for the hypothesis of no overall tree species effect using the reduced dataset. Separate Chi Square tests of equal proportion were computed to determine if abundance of specimens and species richness was dependent on tree species. Species accumulation curves, using the full dataset, comparing sample number and number of accumulated species were plotted with Microsoft® Excel® to examine trends in species richness and visually evaluate sampling efficiency.

To analyze turnover rate (**Objective 2,** in part), the full dataset was utilized. Decay week-to-decay week similarities were computed using Chao's abundance-based Jaccard indexes in the statistical freeware EstimateS (Colwell 2005). According to the EstimateS user's guide,

> *"Chao's Abundance-based Jaccard indexes are based on the probability that two randomly chosen individuals, one from each of two samples (quadrats, sites, habitats, collections, etc.), both belong to species shared by both samples (but not necessarily to the same shared species). The estimators for these indexes take into*

account the contribution to the true value of this probability made by species actually present at both sites, but not detected in one or both samples. This approach has been shown to reduce substantially the negative bias that undermines the usefulness of traditional similarity indices, especially with incomplete sampling of rich communities (Chao et al. 2005). EstimateS 7.5+ computes the raw Chao Abundance-based Jaccard indexes (not corrected for undersampling bias) as well as the estimators of their true values, so that you can assess the effect of the bias correction on the indexes."

The raw and estimated Chao abundance-based Jaccard indexes (similarity values) were graphed on the secondary y-axes of succession diagrams displaying the number of total taxa and new arrivals collected on each tree species and season similar to the method used by Schoenly and Reid (1987). Means of the estimated Chao abundance-based Jaccard index revealed turnover rate differences between loblolly pine and southern red oak bolts.

To determine the patterns in species assemblages (**Objectives 2, 3**), the reduced dataset was analyzed using multivariate, principle component analysis (PCA; Proc Factor) and regression analysis (Proc Mixed) (SAS Institute 2004). PCA was used to reduce variables into fewer compound variables called factors with the aim of accounting for the most variance present in initial variables with the least number of factors (*i.e.*, principle components). The SAS software used the eigenvalues greater than 1.0 rule to determine the number of informative factors to retain. The Catell scree test plot shared the same results: eight factors were extracted. The factor structure was simplified and made more interpretable by adding a varimax rotation. Correlations among taxa (dependent variable) and each factor were generated. The correlations, or factor loadings, greater than |0.30| were used to determine which taxa contributed to variation of each factor (ACITS 1995). The MIXED procedure modeled and calculated significance tests for factor scores of eight extracted factors as the dependent variable against the seven class variables (season, week, site, treesp, dup, bolt, and section) and the interactions of interest. The Tukey-Kramer ($P<0.05$) adjustment was used to make pair-wise comparisons among all levels.

CHAPTER 3: RESULTS

The 24 trees felled were shown to be uniform with regard to age and DBH. Type III tests of fixed effects for age and (MIXED procedure) DBH found no effect to be significant (Table 3.1,Table 3.3). Average age and DBH of loblolly pine (henceforth referred to simply as 'pine') was 40.3 years and 30.9 cm, respectively. Average age and DBH of southern red oak (henceforth referred to simply as 'oak') was 43.4 years and 28.3 cm, respectively (Table 3.2, Table 3.4).

Table 3.1. Analysis of variance results determining whether the age (yrs) of felled Loblolly Pine and Southern Red Oak trees differ among independent variables and their interaction (N = 24).

Type 3 Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Season	1	4	0.03	0.8727
TreeSp	1	4	1.76	0.2551
Season*TreeSp	1	4	1.4	0.302

No significant differences between tree age and treatment effects were detected.

Table 3.2. Analysis of variance estimates of tree age among given effects and their interaction (N = 24).

Least Squares Means									
Effect	**Tree Sp**	**Season**	**Estimate (years)**	**Standard Error**	**DF**	**t Value**	**Pr > |t|**	**Lower CL**	**Upper CL**
Season		1	42.33	3.80	4	11.15	0.0004	31.79	52.88
Season		2	41.42	3.80	4	10.91	0.0004	30.87	51.96
TreeSp	Oak		43.42	2.93	4	14.84	0.0001	35.29	51.54
TreeSp	Pine		40.33	2.93	4	13.79	0.0002	32.21	48.46
Season* TreeSp	Oak	1	42.50	4.14	4	10.27	0.0005	31.01	53.99
Season* TreeSp	Pine	1	42.17	4.14	4	10.19	0.0005	30.68	53.65
Season* TreeSp	Oak	2	44.33	4.14	4	10.72	0.0004	32.85	55.82
Season* TreeSp	Pine	2	38.50	4.14	4	9.31	0.0007	27.01	49.99

Table 3.3. Analysis of variance results determining whether the DBH (cm) of felled Loblolly Pine and Southern Red Oak trees differ among independent variables and their interaction (N = 24).

Type 3 Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Season	1	4	0	0.9544
TreeSp	1	4	5.14	0.086
Season*TreeSp	1	4	0.13	0.7332

No significant differences between tree age and treatment effects were detected.

Table 3.4. Analysis of variance estimates of tree DBH among given effects and their interaction (N = 24).

Least Squares Means									
Effect	**Tree Sp**	**Season**	**Estimate (cm)**	**Standard Error**	**DF**	**t Value**	**Pr > |t|**	**Lower CL**	**Upper CL**
Season		1	29.59	0.98	4	30.08	<.0001	26.86	32.32
Season		2	29.68	0.98	4	30.16	<.0001	26.94	32.41
TreeSp	Oak		28.32	0.91	4	31.29	<.0001	25.81	30.83
TreeSp	Pine		30.95	0.91	4	34.19	<.0001	28.43	33.46
Season*TreeSp	Oak	1	28.07	1.28	4	21.93	<.0001	24.51	31.62
Season*TreeSp	Pine	1	31.12	1.28	4	24.31	<.0001	27.56	34.67
Season*TreeSp	Oak	2	28.58	1.28	4	22.32	<.0001	25.02	32.13
Season*TreeSp	Pine	2	30.78	1.28	4	24.04	<.0001	27.22	34.33

Insects were observed colonizing felled trees immediately following experiment setup and were abundant beginning with the first sampling event. In addition to Coleoptera, samples contained insects from 11 other orders of class Insecta (Table 3.5). A total of 51,119 adult beetles were collected during the sample months October 2004 – September 2005 (18 sampling events, 3822 samples). The Coleoptera dataset included 35 families and 149 genera. Species richness was 190, based on identified species plus morphospecies (Appendix A). The most species-rich family was Curculionidae (32 spp.; Appendix G, Figure G.1) followed by

Staphylinidae (31 taxa; Appendix G, Figure G.2), Histeridae (17 spp.; Appendix G, Figure G.3), Zopheridae (16 spp.; Appendix G, Figure G.4), and Nitidulidae (14 spp.; Appendix G, Figure G.5). Although the Curculionids were the most species-rich, the Scolytine subfamily was not as abundant in individuals as the second most species-rich family, Staphylinidae. The majority of individuals belonged to reduced dataset of 30 taxa from 11 families and 22 genera (Appendix B,

Table 3.5. List of 11 non-coleopteran insect orders based on adults collected from freshly killed Loblolly Pine and Southern Red Oak trees from samples spanning October 2004 - September 2005 at Feliciana Preserve, West Feliciana Parish, LA.

Order	**Family**	**Taxa**
BLATTARIA	morphospecies 1	
COLLEMBOLA	Entomobryidae	
	Hypogastruridae	
	Sminthuridae	
DERMAPTERA	morphospecies 2	
DIPTERA	Dolichopodidae	
	Lonchaeidae	
	Mycetophilidae	
	Phoridae	
	Sciaridae	
HEMIPTERA	Aphididae	
	Aradidae	*Mezira sayi* Kormilev
	Enicocephalidae	*Systelloderes* sp.
	Largidae	*Largus succinctus* (L.)
	Miridae	
HYMENOPTERA	Formicidae	*Aphaenogaster* sp.
	Formicidae	*Camponotus* sp.
	Formicidae	*Crematogaster* sp.
	Formicidae	*Pheidole* sp.
	micro-Hymenopteran 1	
	micro-Hymenopteran 2	
	micro-Hymenopteran 3	
ISOPTERA	Rhinotermitidae	*Reticulitermes virginicus* (Banks)
MICROCORYPHIA	Meinertellidae	
PSOCOPTERA	morphospecies 3	
THYSANOPTERA	Phloeothripidae	
ZORAPTERA	Zorotypidae	*Zorotypus hubbardi* Caudell

C). Of the remaining 160 taxa, 64 were singletons (31 from pine, 33 from oak) and 15 doubletons (3 from pine, 10 from oak, and 2 with one individual from each pine and oak). Beetles were significantly more abundant (X^2= 1659.7062, P= <.0001) during season 2 than 1 (30,165 and 20,954 individuals respectively; Table 3.6).

Table 3.6. Number of taxa (non-additive) and total specimen abundance collected per season and tree species. Collected taxa for each column were added to that quantity's calculation at first occurrence only. For the remainder of all tables and figures, Pine = Loblolly Pine, Oak = Southern Red Oak.

	Season 1			**Season 2**			**All Samples**		
	Pine	**Oak**	**Total**	**Pine**	**Oak**	**Total**	**Pine**	**Oak**	**Total**
Taxa	61	81	105	102	127	162	122*	144**	190
Abundance	2627	18327	20954	7618	22547	30165	10245	40874	51119

* Number of taxa exclusively on Pine = 46

** Number of taxa exclusively on Oak = 68

3.1 Comparisons between Tree Species – Objective 1

Of 190 taxa, 76 (40.0 %) were collected from both loblolly pine and southern red oak (Table 3.6). Sixty eight taxa (35.8 %) were unique to oak and 46 (24.2 %) were unique to pine. Species composition for the reduced dataset differed significantly between tree species (Wilks' Lambda = 0.41031, P=<0.0001; Table 3.7). Species accumulation curves from the first six

Table 3.7. MANOVA Test Criteria and Exact F Statistics for the Hypothesis of No Overall TreeSp Effect.

Statistic	Value	F Value	Num DF	Den DF	Pr > F
Wilks' Lambda	0.41031	179.6	30	3749	<.0001
Pillai's Trace	0.58969	179.6	30	3749	<.0001
Hotelling-Lawley Trace	1.43718	179.6	30	3749	<.0001
Roy's Greatest Root	1.43718	179.6	30	3749	<.0001

months of Season 1 (Figure 3.1) show that species richness is consistently higher on oak than pine. Species accumulation curves from season 2 (Figure 3.2) also show higher species richness

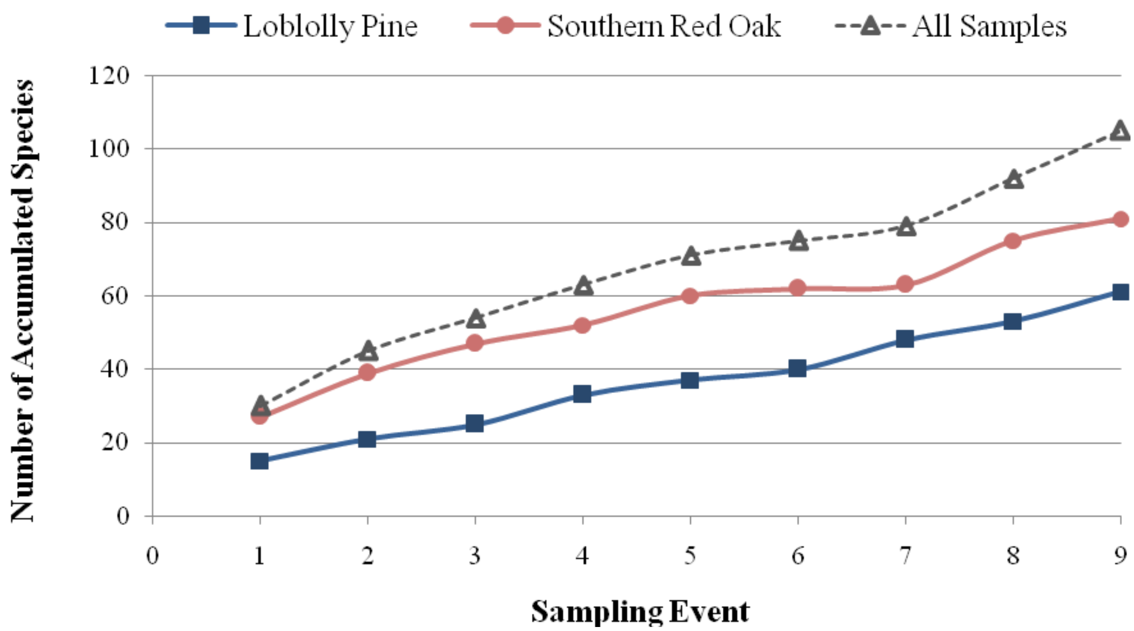


Figure 3.1. Accumulation curves for samples collected during season 1 (in part, October 2004 - March 2005).

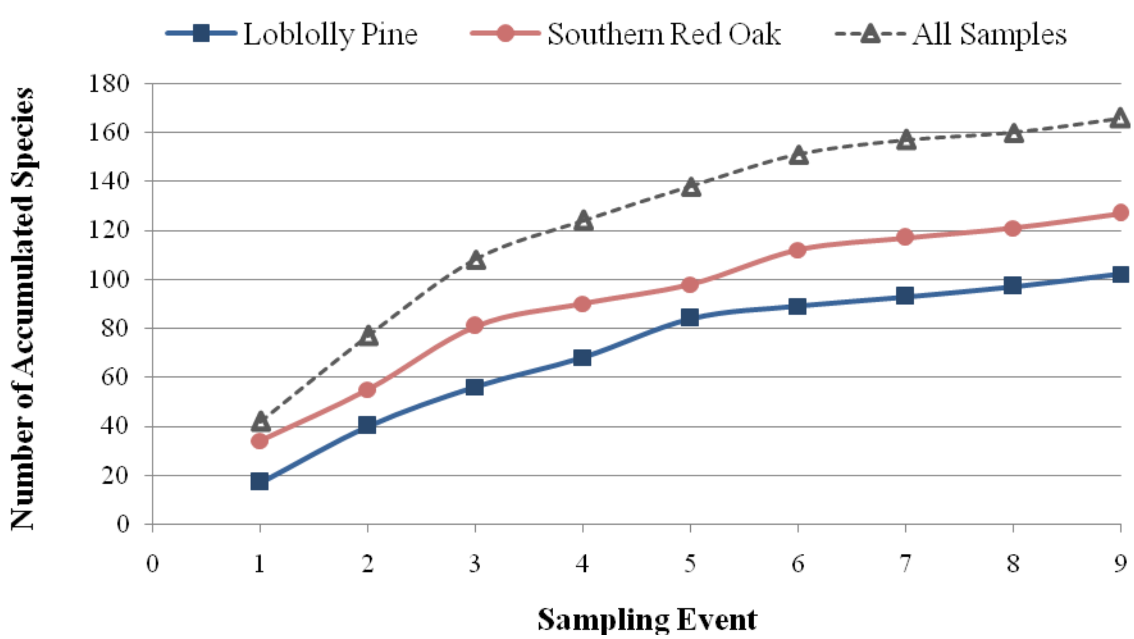


Figure 3.2. Accumulation curves for samples collected during season 2 (April - September 2005).

for oak. Both graphs show that results would have benefitted from additional sampling. Curves for season 2 more closely approximate asymptotic curves representative of high sampling efficiency.

The Chi-Square test of equal proportions determined that species abundance was significantly higher (χ^2 =18351.9952, P=<0.0001; Table 3.8) on oak than pine (40,874 and 10,245 individuals respectively). Species richness was higher on oak than pine, 144 and 122 taxa, respectively, although not significantly so (χ^2=1.8195, P=0.1774; Table 3.9).

Table 3.8. The FREQ Procedure; Abundance tested for significance by TreeSp.

TreeSp	Freq	Cum Freq
Oak	40874	40874
Pine	10245	51119

Chi-Square Test for Equal Proportions	
Chi-Square	18351.9952
DF	1
Pr > ChiSq	<.0001

Table 3.9. The FREQ Procedure; Species Richness tested for significance by TreeSp.

TreeSp	Frequency
Oak	144
Pine	122

Chi-Square Test for Equal Proportions	
Chi-Square	1.8195
DF	1
Pr > ChiSq	0.1774

3.2 Arrival Sequence – Objective 2, in part

Frequency data for the reduced dataset were used to display the arrival sequences of the 30 most abundant taxa during season 1 and season 2 (Table 3.10, Table 3.11, respectively).

Table 3.10. Succession of 30 most abundant Coleoptera on Loblolly Pine and Southern Red Oak bolts during season 1 (in part, October 2004 - March 2005).

			Decay Week								
	Taxa		**1**	**2**	**3**	**4**	**8**	**12**	**16**	**20**	**24**
Carabidae	*Mioptachys flavicauda*	Pine			2	3			1		
		Oak	1	1		1		1		1	1
Cerylonidae	*Cerylon unicolor*	Pine							1	1	
		Oak			1		1	1	2		3
Curculionidae	*Cossonus corticola*	Pine	1	11	59	60	5	2	1	1	
		Oak	1			2	1	1			
	Cossonus impressifrons	Pine									
		Oak								2	1
	Xyleborinus saxeseni	Pine	2	2	2	1		1		1	
		Oak	1			1					
	Xyleborus affinis	Pine							1		
		Oak	26	6	2	1					
Histeridae	*Aeletes floridae*	Pine	87	117	44	18	11	9	23	24	36
		Oak	160	214	259	183	145	188	554	1230	914
	Bacanius punctiformis	Pine									
		Oak									
	Platysoma coarctatum	Pine		1	1	9	2	1		4	1
		Oak		3	12	4	1			7	3
	Platysoma lecontei	Pine	1						1		
		Oak	1		4	4			10	15	20
	Platysoma parallela	Pine			1	1	1				
		Oak									
	Plegaderus transversus	Pine									
		Oak							1		
Laemophloeidae	*Phloeolaemus chamaeropis*	Pine									
		Oak	13	49	78	28	5	17	18	6	2

Table 3.10. continued

Nitidulidae	*Carpophilus corticinus*	Pine	14	31	23	16	4	3	3	1	
		Oak	53	90	65	35	1	2	2	1	
	Carpophilus tempestivus	Pine									
		Oak	52	86	68	14	1		3	5	
	Colopterus niger	Pine									
		Oak	113	148	113	80	4	1	2	3	
	Colopterus semitectus	Pine									
		Oak	7	2	2						1
	Colopterus truncatus	Pine	1	3							
		Oak	93	40	24						
	Epuraea erichsoni	Pine	3		1		2	2			
		Oak	49	88	58	18					
Ptiliidae	Ptiliidae spp.	Pine									
		Oak				1					
Silvanidae	*Silvanus muticus*	Pine	27	34	31	11	321	237	62	49	48
		Oak	40	64	51	37	83	52	65	38	72
Staphylinidae	*Laetulonthus laetulus*	Pine	2								
		Oak	1		4	7	1			1	
	Leptusa spp.	Pine				1	1	2	4	6	3
		Oak		1			1		4	26	11
	Myrmecocephalus concinnus	Pine	54	29	9	10	66	16	26	4	5
		Oak	83	77	50	45	72	42	44	34	17
	Placusa sp.	Pine	230	176	81	27	117	8	27	12	11
		Oak	2858	2195	2792	1930	850	315	250	38	22
	Thoracophorus costalis	Pine									
		Oak		1	1	4	2	2		1	
Tenebrionidae	*Corticeus glaber*	Pine									
		Oak									
Zopheridae	*Bitoma quadricollis*	Pine									
		Oak					2	1	55	17	
	Pycnomerus haematodes	Pine						1			
		Oak									

Table 3.11. Succession of 30 most abundant Coleoptera on Loblolly Pine and Southern Red Oak bolts during season 2 (April - September 2005).

			Decay Week								
	Taxa		**1**	**2**	**3**	**4**	**8**	**12**	**16**	**20**	**24**
Carabidae	*Mioptachys flavicauda*	Pine	1	2	13	5	37	50	98	107	230
		Oak	4	9	10	4	20	47	130	129	177
Cerylonidae	*Cerylon unicolor*	Pine		2	6	2	23	36	30	42	29
		Oak	3	6	14	16	37	72	82	71	46
Curculionidae	*Cossonus corticola*	Pine		9	78	400	1901	334	117	17	21
		Oak								1	1
	Cossonus impressifrons	Pine					1	3	2		2
		Oak					327	983	234	16	
	Xyleborinus saxeseni	Pine	10	57	93	43	7	1			
		Oak	6	9	4	4	1				
	Xyleborus affinis	Pine		1	4						
		Oak		73	13	4					
Histeridae	*Aeletes floridae*	Pine	83	207	84	42	103	21	2		2
		Oak	504	505	208	336	1242	961	257	59	
	Bacanius punctiformis	Pine							2		11
		Oak			1		89	131	51	44	36
	Platysoma coarctatum	Pine		8	1	4	10	5			
		Oak		1	1			4	1		
	Platysoma lecontei	Pine		2	3	2		1		2	3
		Oak	15	7	19	18	24	28	11	8	3
	Platysoma parallela	Pine		14	57	42	2	4			
		Oak									
	Plegaderus transversus	Pine		1	5	76	233	1			
		Oak									
Laemophloeidae	*Phloeolaemus chamaeropis*	Pine		1							
		Oak	68	235	220	142	33	3	1	1	

Table 3.11. continued

Nitidulidae	*Carpophilus corticinus*	Pine	6	6		11	3				
		Oak	31	28	22	7					
	Carpophilus tempestivus	Pine									
		Oak	264	168	75	4					
	Colopterus niger	Pine									
		Oak	135	139	113	15	1				
	Colopterus semitectus	Pine									
		Oak	146	82	18						
	Colopterus truncatus	Pine									
		Oak	136	59	8						
	Epuraea erichsoni	Pine				1					
		Oak	9	8	1						
Ptiliidae	Ptiliidae spp.	Pine					93	7	94	46	18
		Oak			1		55	158	148	387	23
Silvanidae	*Silvanus muticus*	Pine	175	182	167	82	98	154	55	31	12
		Oak	277	325	218	156	196	245	116	89	16
Staphylinidae	*Laetulonthus laetulus*	Pine	1	3	5	5					
		Oak	26	46	14	4					
	Leptusa spp.	Pine			9	36	2				
		Oak		2			3				
	Myrmecocephalus concinnus	Pine	15	27	17	24	4	5			
		Oak	24	103	57	91	14	44	1		
	Placusa sp.	Pine	195	110	76	86	5	4			
		Oak	2924	3007	1563	482	27	7			
	Thoracophorus costalis	Pine				1		2	3	11	14
		Oak	5	3	7	10	15	15	6	15	26
Tenebrionidae	*Corticeus glaber*	Pine		27	124	47	3	2	1		
		Oak									
Zopheridae	*Bitoma quadricollis*	Pine		1							
		Oak		3	22	12	12	3	1		
	Pycnomerus haematodes	Pine					1	2	7	29	37
		Oak				1		2	2	2	8
	Pycnomerus reflexus	Pine				2	5	16	13	29	71
		Oak	2	20	41	49	213	216	407	366	229

Beetle taxa succession patterns were identified by determining species' presence from week to week during each season and for each tree species. A visual assessment shows that beetles did indeed colonize trunks rapidly within the first week of felling. Twenty-seven of the 30 taxa were collected from pine. After the first week of decay, pine bolts were colonized by ten taxa during season 1 in the families Curculionidae, Histeridae, Nitidulidae, Silvanidae and Staphylinidae. Season 2 pine bolts were colonized early by eight taxa in the same families but included the Carabid, *Mioptachys flavicauda* (Say). Twenty-eight of the 30 taxa were collected from oak. Succession patterns for oak show 17 and 18 taxa arriving during week 1 of season 1 and 2, respectively. The first week of colonization on oak bolts began with Carabidae, Curculionidae, Histeridae, Laemophloeidae, Nitidulidae, Silvanidae and Staphylinidae during season 1 and 2, but the latter was additionally visited by the Cerylonid, *Cerylon unicolor* (Ziegler), and the Zopherid, *Pycnomerus reflexus* Say.

The most notable colonization record was for the most abundant taxon, *Placusa* sp. (Appendix G, Figure G.2). Samples of *Placusa* sp. collected after pine and oak bolts decayed for one week accounted for 77.3 % of all collected beetles (3088/3995 total individuals) during season 1 and 60.9 % (3119/5122 total individuals) during the same decay week in season 2. Another notable record was held by *Silvanus muticus* Sharp. It was the **only** species that was collected during both seasons, on both tree species, and during every decay week. It was also the third most abundant species throughout both seasons. *Aeletes floridae* (Marseul) was the second most abundant species and persisted in season 1 on both tree species during every decay week and in season 2 on both species, except for week 20 (found only on oak) and 24 (found only on pine). Statistical results comparing unifying factors in succession patterns among species assemblages are presented in section 3.4 below.

Succession diagrams of the total number of taxa and number of new arrivals per decay week and season for each tree type (Figure 3.3, Figure 3.4) incorporate the Chao-Jaccard raw and estimated abundance-based indexes. The turnover of species week to week across seasons for oak was slightly more similar (estimated index mean= 0.9459) than pine (estimated index mean=0.9235), thus oak had a more gradual succession sequence than pine. Beetle taxa reached maximum richness on pine bolts at the 20^{th} week of decomposition during season 1 and at week 3 during season 2. On oak bolts, maximum richness was reached equally at week 2 and 24 during season 1 and at week 3 during season 2. The number of taxa colonizing and arriving at each tree species increased gradually with intermittent decreases during both seasons.

3.3 Succession Patterns by Tree Species and by Season – Objectives 2, 3

Using frequency data for the 30 most abundant beetle taxa and seven independent variables described earlier (refer also to Class Information, Appendix E, Table E.1), eight factors were extracted in the FACTOR procedure. Factor loadings, or correlations, greater than |0.30| were considered significant and determined which taxa where grouped together in 'factors' or beetle assemblages (Appendix D). The MIXED procedure was conducted with the dependent variable 'factor score' (generated by the FACTOR procedure) and resulted in Type III tests of fixed effects for the seven independent variables (*i.e.,* treatments) and selected interactions (Table 3.12; Appendix E). Succession patterns were gauged by the significant interactions WEEK*TREESP (Table 3.13), WEEK* SEASON (Table 3.14), and SEASON*WEEK*TREESP (Table 3.15) and the significant log-abundance LSMeans estimates (Appendix E). Both second-order interaction effects were highly significant (P=<0.001). In fact, any effect that included week was highly significant. Because the third-order interaction was also significant, the results for succession patterns reflected findings for the term.

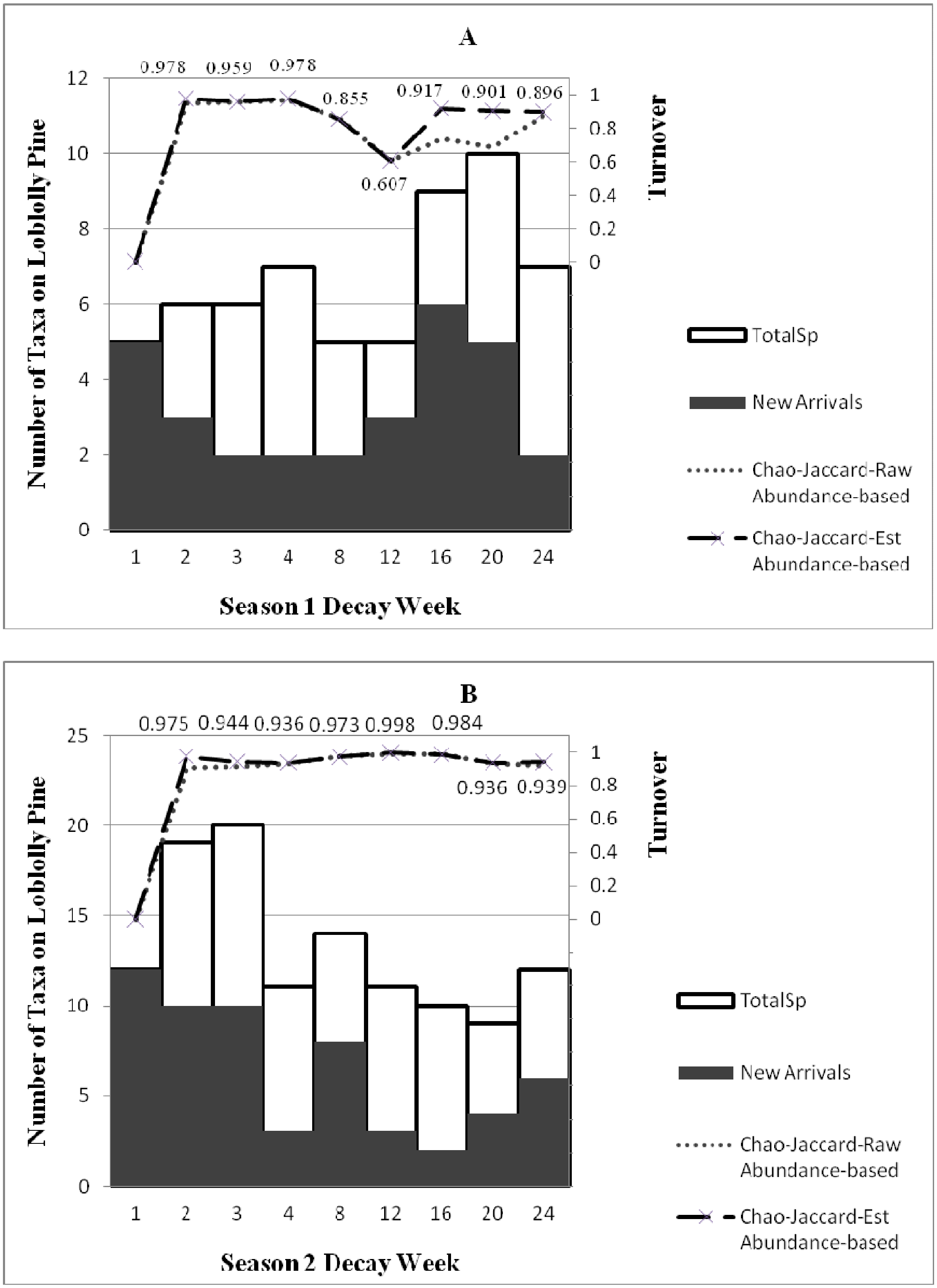
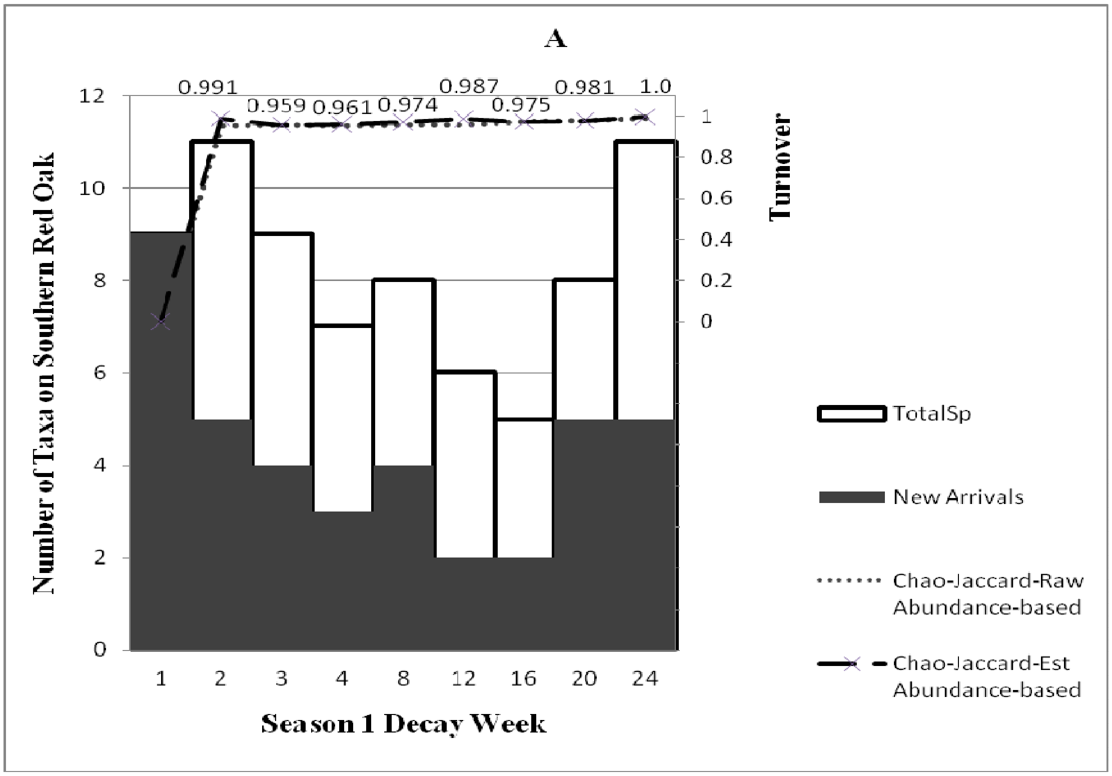


Figure 3.3. Succession diagrams of taxa collected on Loblolly Pine during A) season 1 and B) season 2. The two top lines are turnover rates for each pair of decay weeks (range 0-1). Lower histograms display number of new arrivals and total species.



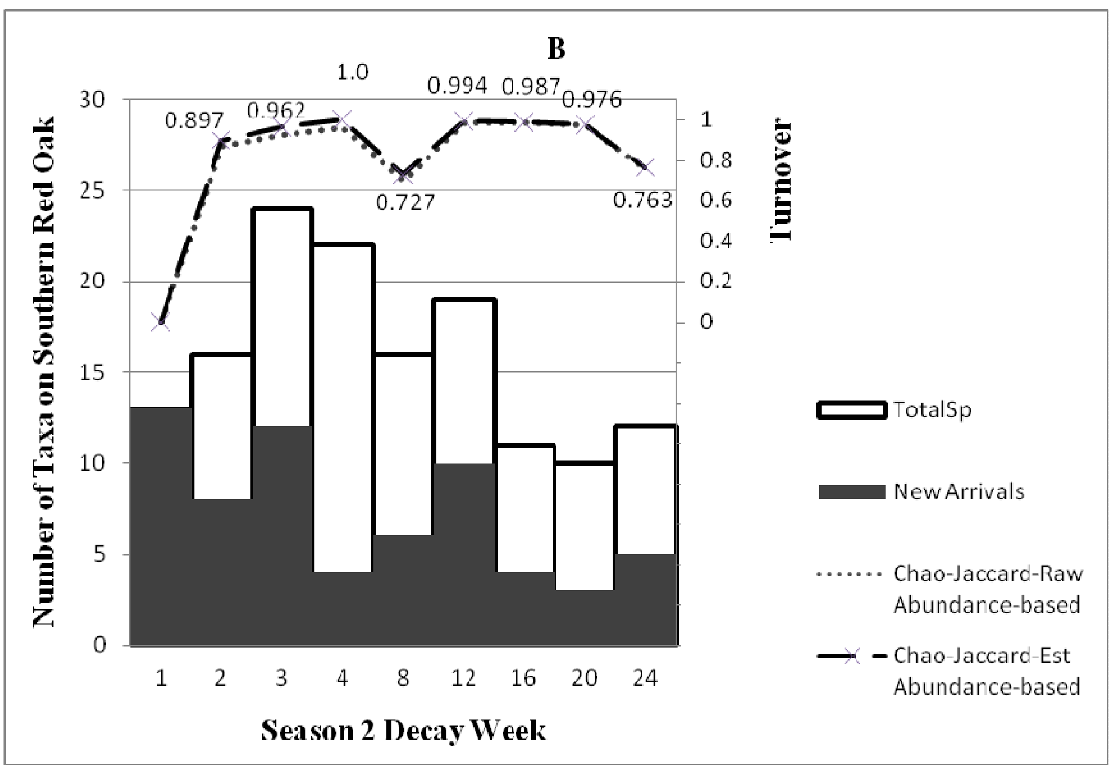


Figure 3.4. Succession diagrams of taxa collected on Southern Red Oak during A) season 1 and B) season 2. The two top lines are turnover rates for each pair of decay weeks (range 0-1). Lower histograms display number of new arrivals and total species.

Table 3.12. Regression analysis Type III tests of fixed effects. P-values are given for factors completing analysis.

Factor	Season	Tree Sp	Season* TreeSp	Bolt	Section	Week	Season *Week	Week* TreeSp	Season *Week *Tree Sp
1	**0.0003**	**0.0037**	**0.0065**	0.0825	**0.0431**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
2	**0.0063**	**0.0008**	**0.0398**	0.0618	0.0809	**<.0001**	**<.0001**	**<.0001**	**<.0001**
3	analysis stopped because of infinite likelihood								
4	analysis stopped because of infinite likelihood								
5	**0.0193**	**0.0182**	**0.0282**	0.9198	0.1391	**<.0001**	**<.0001**	**<.0001**	**<.0001**
6	**0.0315**	**0.0089**	**0.0186**	0.7497	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
7	0.4011	**0.0004**	**0.0049**	0.8159	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
8	analysis stopped because of infinite likelihood								

Table 3.13. Most significant WEEK*TREESP LSMeans comparisons. Tukey-Kramer values for each comparison are the most significant log-abundance estimates and are in group 'A'.

Factor	Week	TreeSp	Estimate	Standard Error	DF	t Value	Pr > |t|
1	12	Oak	0.8679	0.06583	3358	13.18	<.0001
1	16	Oak	0.8291	0.06622	3358	12.52	<.0001
1	20	Oak	0.7235	0.06583	3358	10.99	<.0001
2	1	Oak	2.122	0.06245	3358	33.98	<.0001
5	3	Pine	1.5007	0.08627	3358	-0.24	0.8118
6	8	Pine	1.8496	0.08649	3358	-2.01	0.0441
7	12	Oak	1.1582	0.07588	3358	2.68	0.0075

Table 3.14. Most significant WEEK*SEASON LSMeans comparisons. Tukey-Kramer values for each comparison are the most significant log-abundance estimates.

Factor	Week	Season	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
1	1	1	-0.3809	0.07053	3358	-5.4	<.0001	A
1	2	1	-0.4008	0.06583	3358	-6.09	<.0001	AB

Table 3.14 continued

1	3	1	-0.4218	0.06583	3358	-6.41	<.0001	AB
2	1	2	1.5046	0.06453	3358	4.87	<.0001	A
5	3	2	1.4457	0.09031	3358	-1.34	0.1788	A
6	8	2	1.6834	0.08761	3358	-2.48	0.0131	A
7	12	2	0.9306	0.08948	3358	-1.11	0.267	A
7	8	2	0.7123	0.08443	3358	-0.88	0.3788	A

Table 3.15. Most significant WEEK*TREESP*SEASON LSMeans comparisons, arranged chronologically. Tukey-Kramer values for each comparison are the most significant log-abundance estimates.

Factor	Week	Tree Sp	Season	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
2	1	Oak	2	3.2338	0.09536	3358	10.59	<.0001	A
5	3	Pine	2	3.1934	0.1274	3358	-0.44	0.661	A
6	8	Pine	2	3.811	0.1263	3358	-1.7	0.0887	A
7	12	Oak	2	2.2494	0.113	3358	-1.45	0.146	A
1	12	Oak	2	2.209	0.1025	3358	-2.51	0.012	A
1	16	Oak	2	2.1491	0.09692	3358	-5.2	<.0001	AB

3.4 Species Assemblages

The first assemblage (Appendix F) included *Pycnomerus reflexus*, *Bacanius punctiformis*, *Cerylon unicolor*, *Mioptachys flavicauda*, Ptiliidae spp., *Cossonus impressifrons*, and *Thoracophorus costalis*. This assemblage had the most significant factor for SEASON (P=0.0003). All associated beetle taxa were more abundant during season 2 collected from oak. Taxa were more abundant on section 6 and were prevalent during weeks 16, 20, 12, 24 (in descending significance). Significance was also noted in taxa collected from week 16 of season 2, weeks 12, 16, 20 of season 2 from oak; and from oak in general during week 12.

Assemblage 2 consisted of *Colopterus semitectus*, *Carpophilus tempestivus*, *Colopterus* *truncatus*, *Colopterus niger*, and *Placusa* sp. Assemblage 2 had the second most significant factor for SEASON (P=0.0063) and TREESP (P=0.0008). Taxa were more abundant in season 2. Three taxa were collected exclusively from oak, and the other two were collected over 94 % from oak. The four taxa with the most significant factor loadings were all Nitidulidae. Taxa were most prevalent during week 1, especially colonizing oak trees during season 2.

The third assemblage was made up of seven taxa, Phloeolaemus *chamaeropis*, *Myrmecocephalus concinnus*, *Silvanus muticus*, *Xyleborus affinis*, *Aeletes floridae*, *Laetulonthus laetulu*s, *Placusa* sp., and *Carpophilus tempestivus*. Although the MIXED procedure was unable to complete analysis of this assemblage, it was noted that an average of 75% of specimens from the associated taxa were collected from oak in this factor. Six of eight taxa were more numerous in season 2. Many specimens were collected during week 1, 2, 3, and 4.

Several taxa had characteristics that placed them in more than one assemblage (*e.g., Placusa* sp.). Beetle assemblage four also contained *Placusa* sp., as well as *Epuraea erichsoni*, *Carpophilus corticinus*, *Colopterus niger*, and *Myrmecocephalus concinnus*. The MIXED procedure was also unable to complete analysis of this assemblage, yet it was noted that all taxa were significantly more abundant on oak during season 1. Many specimens from the three taxa demonstrating the most significant factor loadings occurred during from week 1-4. The five associated taxa are from two beetle families: Nitidulidae and Staphylinidae.

Assemblage five was made of four taxa (*Corticeus glaber*, *Platysoma parallela*, *Xyleborinus saxeseni*, and *Leptusa* spp.). Associated taxa were significantly more abundant during week 3 of season 2 from pine. The two taxa with the most significant factor loadings were collected exclusively from pine.

Assemblage six is categorized as a doublet because only two taxa were associated with it, *Cossonus corticola* and *Plegaderus transversus*. Both species were significantly more numerous from pine (over 95 % of specimens), section 6, during season 2. Taxa were strongly associated with pine during week 8 and with pine during season 2.

Assemblage seven consisted of *Aeletes floridae, Cossonus impressifrons, Platysoma lecontei, Silvanus muticus, Pycnomerus haematodes,* and *Mioptachys flavicauda.* This assemblage is the most significant for TREESP (P=.0004), SEASON*TREESP (P=.0049), and SECTION (P=<0.0001). Taxa corresponding to positive loadings were significantly more numerous on oak, section 6, in season 2. Taxa corresponding to negative loadings were similar in being found in season 2, but *contrasted* by being slightly more abundant on pine bolts. Overall, taxa were significantly linked to section six, weeks 12 and 8, season 2 week 12 and season 2 week 8, as well as the combination of season 2 week 12 and oak.

Three taxa made up assemblage eight: *Leptusa* spp., *Bitoma quadricollis*, and *Platysoma coarctatum*. The MIXED procedure was also unable to complete analysis of this factor. All three taxa were more abundant in season 2. Main separation for this factor seems to be a tricky interaction of season and week collected: season 1, later weeks (16, 20) and season 2, early weeks (3, 4, and 8).

Evaluating only the third-order interaction WEEK*TREESP*SEASON, all beetle assemblages that completed analysis were most abundant during season 2 (Table 3.15). Chronologically, assemblage 2 arrived first and was most abundant on oak bolts during the first week of decay (Figure 3.5). Assemblage 5 was most abundant on pine bolts during week 3. Assemblage 6 then arrived most abundantly during week 8 also on pine. Assemblage 7 arrived most abundantly during week 12 on oak, except for *Pycnomerus haematodes* (F.) and

Mioptachys flavicauda (Say), which were slightly more abundant on pine. Assemblage 1 was equally abundant during weeks 12 and 16 on oak bolts.

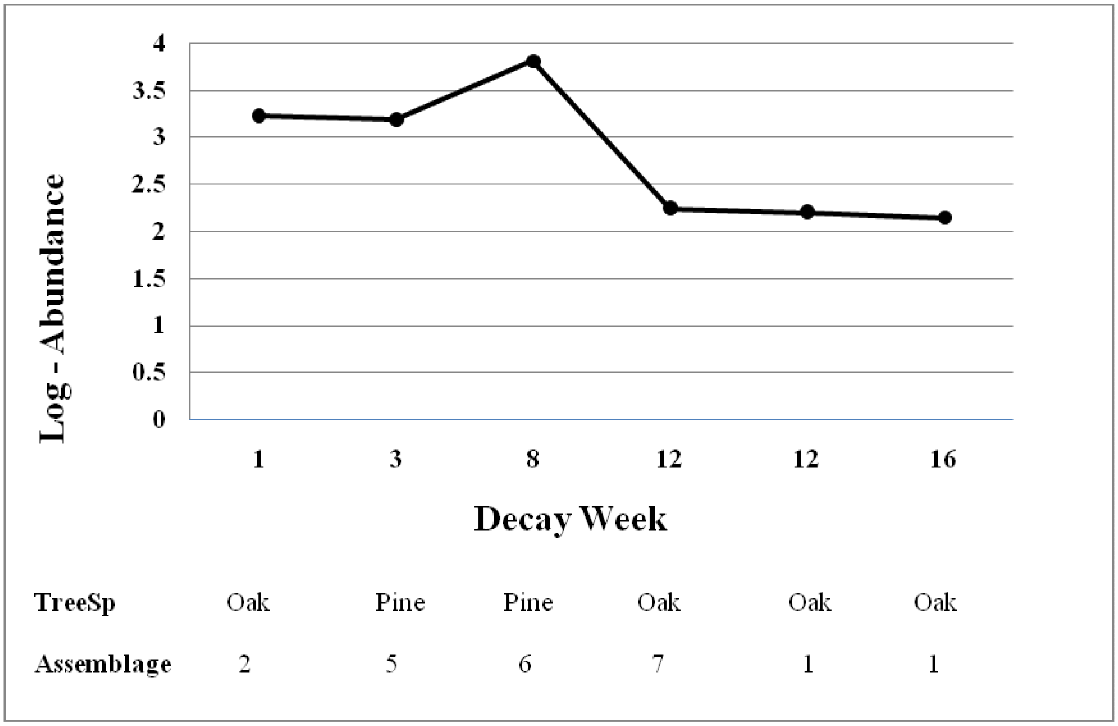


Figure 3.5. Log-abundance of the most significant WEEK*TREESP*SEASON comparisons, arranged chronologically by tree species and assemblage.

CHAPTER 4: DISCUSSION

The general purpose of this research project was to document beetle succession of felled loblolly pines and southern red oaks by determining which species of beetles colonize freshly killed standing bolts and the sequence of each species' arrival. Cutting the bolts into six-inch, movable sections alleviated the necessity for destructive sampling. Section pieces were lifted, insects sampled, and then replaced. A side effect of having many cuts in the bolt was loss of moisture. This loss was not quantified, and therefore its true effect cannot be known. Bark began to loosen more readily on pine than oak. This artifact of experimental setup may have deterred beetles requiring more moisture to colonize. For less sensitive taxa, given that it occurred equally throughout the woody substrates, the reliability of the results should not be vastly affected, and may have simply accelerated the normal processes of occupancy and succession.

While no particular taxon was targeted when designing the experiment, it was expected that known saproxylic beetles distributed in Louisiana would be prevalent in samples. The beetle families Curculionidae, Buprestidae, and Cerambycidae typically initiate attacks against freshly killed trees (Harmon *et al*. 1986; Zhong and Schowalter 1989; Savely 1939). Beetles began visiting the felled trees soon after experimental setup. In October 2004, during season 1, a female Cerambycidae was observed on the outer bark of an oak tree within 24 hours of tree felling. Wood-boring beetles were infrequent (or completely absent as was the case with Buprestidae) in samples due to the short height of bolts (48-inches). Regarding host selection behavior and colonization habits of Scolytines, Drooz (1985) noted:

> *"Generally, [*Scolytine*] beetles attack the middle and upper trunk first, especially in the Middle Atlantic States. Later they continue their attacks* ***down the trunk to within 1.5 m*** *or less of the ground. In the Deep South, overwintering adults emerge during warm periods in the winter and may attack the upper and lower*

portions of the tree from which they emerged. However, most of these beetles emerge in late February or early March and first attack the mid to lower trunk of new host trees. Continuing attacks extend the zone of attack down to the ground line and up in the base of the live crown."

In addition to the missing height of a vertical silhouette preferred by Scolytines it is also possible that some landed on the bark but did not colonize given the rapidly drying sections of the bolts. Harmon *et al.* (1986) wrote that "both extremely low and high moisture content can limit the activity of organisms." Howden and Vogt (1951) noted that the insect community in severed, standing Virginia pine was very different than downed logs because the logs contained more moisture.

Besides beetles, insects from 11 other orders visited or colonized the bolts. This is expected as many saproxylic beetles populating wood attract the presence of opportunistic and predatory insects (Camors and Payne 1972). Formicidae were a definite component of change. Once they settled in a bolt, they usually stayed permanently. Debris of exoskeletons, and colony rubbish were the first indications that ants moved into a section. Another component of change and succession was Isoptera. In contrast to the steady shift of ants to the highest interface of the bolt, termites consistently populated and made trails across the lower two sections of bolts. When these two taxa entered the system, the samples of beetles on bolts appeared to decrease.

4.1 Differences between Tree Species

A multiple analysis of variance comparing beetle species composition patterns present on freshly severed bolts of loblolly pine and southern red oak resulted in a significant difference for the test of tree species overall effect. Species composition patterns did differ between tree species. Specimen abundance was significantly higher on oak. Species richness on oak was higher but not significantly so. Characteristics of each tree species presumably affected the arrival rate and host selection of colonizing beetles. Pine species in good health exude oleoresin and are able to "pitch out" and impede attacking beetles (Dunn and Lorio 1992). Although these trees were felled and therefore unable to produce oleoresin throughout its decay, the section interfaces did exude some sap when the bolts were first felled and cut. The deterrent effects of that sap, if effective at all, would likely have an effect on beetles only during the first week, after which point the sap dried. Qualitatively, oaks were observed to retain much more moisture than pine and to support a greater abundance of fungi, a common food source for saproxylic coleoptera.

4.2 Arrival Sequence and Turnover between Tree Species

Species succession patterns over time were different between tree species. After the first week of decay, oak bolts were colonized by nearly twice the number of taxa as pine bolts. Although there was an overlap in succession sequences between tree species, there were also some taxa that arrived and did not colonize both tree species are at least not at the same density (e.g., Nitidulidae, Laemophloeidae, and Tenebrionidae taxa). Nitidulidae were present on both tree species but were vastly abundant on oak bolts. The laemophloeid, *Phloeolaemus chamaeropis* was almost exclusively collected from oak. Only one specimen was collected from pine bolts. *Corticeus glaber* (Tenebrionidae) were found exclusively on pine bolts and are known facultative predators on southern pine beetle eggs, first and second instar larvae, and theire frass and blue-stain fungus (Berisford 1980). Conversely, many taxa persisted on both tree species week to week once they arrived *(e.g., Aeletes floridae*, *Silvanus muticus*) while others were present in quite abundant numbers and suddenly departed (*e.g.*, *Placusa* sp. after week 12, season 2). Howden and Vogt (1951) studied Virginia pine snags and found that scolytines were the primary invaders and the single most numerous group. In this study, Curculionids were the most species-rich family but the subfamily Scolytinae were not the most abundantly collected taxon. It is important to recall that only adult beetles were classified and included in analyses. It is possible that Scolytines would be more abundant if the larvae were included. Of the reduced dataset, *Xyleborinus saxeseni* was present on both tree species during decay week 1 of both seasons and persisted on average through the 12th decay week. Staphylindae were the most persistent colonizers. Staphylinids such as *Placusa* sp., the most abundant taxon, are not wood-feeders but are saproxylic because they live under bark and feed on other saproxylic species (Speight 1989). *Placusa* spp. are common in eastern forests and prey upon bark beetle eggs, first instars, and small wood-borer larvae (Drooz 1985).

Beetle taxa reached maximum richness after similar periods of decay on both tree species during season 1 and 2. Bolts felled and cut in October displayed maximum richness late in the season (weeks 20, 24) and for oak, richness was equally high after the 2nd week of decay. Bolts felled and cut in April displayed maximum richness early in the season (weeks 3) for both tree species. Similar results were found by Hines and Heikkenen (1977), who detected mass attacks of saproxylic beetles during the second week of decay for trees severed from April to June. This coincides with the mid-April emergence of many overwintering bark beetle taxa (Drooz 1985). Severed loblolly pines showed a slightly more rapid turnover of beetle complexes, whereas turnover in southern red oak bolts was more gradual. Similarities between oak residents were slightly higher than pine residents.

4.3 Succession Patterns by Tree Species and by Season

Multivariate analysis grouped taxa into assemblages based on latent variables, or constructs, deduced from the original set of variables. Eight beetle assemblages (see Appendix F for descriptions of significant effects). Beetle assemblages with similar feeding habits were common (*e.g.,* assemblage 2 and 3) and with future analyses based on feeding guilds, could explain some unifying properties of their cohort overlooked by assessment of season and week abundances. Species succession patterns were different between tree species and between trees felled in early fall and mid-spring based on the regression analysis. The effect of tree species on succession patterns may signify the impact physical and chemical factors have in bolts (Zhong and Schowalter 1989). Differences in plant properties such as loss of moisture, causing loose bark on pines, and higher quality substrate hardwood in oaks certainly influenced the specimen abundance and species composition differences seen between tree types and season in which trees were felled.

Host selection of colonizing beetles was affected by the short height of bolts. Many bark beetles, which prefer *Pinus* hosts, only attack the mid- to upper boles of trees (Drooz 1985). Thus, species richness on pine bolts was low compared to southern red oak. Oak bark remained intact and was able to retain higher moisture content than pine. Additionally, oaks were observed to support a greater abundance of fungi, common food sources for saproxylic coleoptera. Wood feeders are usually limited to one host species or genus (Hanula 1996). As the tree decays, insects change from hostplant specificity to habitat (*i.e.*, condition of CWD decay) specificity (Harmon *et al*. 1986). Saproxylic beetles collected in this study was mainly predators and fungivores, not wood feeders, and were likely not specialized on this hostplant but on the food sources found on the hostplant.

A combination of phloem availability, temperature, relative humidity, and other environmental conditions likely caused succession patterns of saproxylic coleoptera to differ between seasons of tree felling (Graham 1925; Hanula 1996). Seasonal differences in invertebrate abundance and activity on bark have been recognized in other studies (Hanula and Franzreb 1998; Majer *et al*. 2003).

4.4 Species of Interest

Here I discuss taxa with noteworthy life histories, or those infrequently found in Louisiana.

4.4.1 Carabidae: *Mochtherus tetraspilotus* (MacLeay)

Most carabids are known to be predators and this species is no exception. It can be distinguished by the setulose pronotum that is wider than the head, the elytra each with two pale orange spots, and with elytral interval 3 with two punctures (Choate 2001). Adults of *M. tetraspilotus* have been observed scurrying around on recently felled logs (Darlington 1968, Choate 2001). The single specimen obtained in this study was collected on loblolly pine two weeks after felling in season 1 (October18, 2004). *Mochtherus tetraspilotus* (Appendix G, Figure 6) inhabits Japan, Burma, Philippines, Laos, Taiwan, Borneo, Java, Ceylon, India (Jedlicka 1963, Habu 1967), Sri Lanka (Bengtson 2005), and Australia (Calder 2002). The first United States collections were in 1992 from Palm Beach Co., Highlands Co., and Alachua Co., FL (Choate 2001). This species was previously collected in LA in the New Orleans East area (J. Howard, pers. comm.). This study confirms that *M. tetraspilotus* has expanded its range further north in Louisiana.

4.4.2 Cerambycidae: Multiple Species

Wood-borers are known to visit freshly dead trees (Harmon *et al*. 1986; Zhong and Schowalter 1989; Savely 1939). Most of the species (Table 4.1) were collected during the first month of decomposition. Savely (1939) observed *Acanthocinus nodosus* (F.) more abundantly in pine stumps rather than logs. *Asemum striatum* (L.) is a common eastern species that breeds in the sapwood and heartwood of the stumps or lower portions of felled or dying trees, respectively (Drooz 1985). *Cyrtinus pygmaeus* (Halderman) larvae are known to feed on dry branches of hardwoods, including oaks (Lingafelter 2007). *Stenodontes dasytomus dasytomus* (Say) breeds in the heartwood of living hardwood trees, including oaks. It also attacks wood on the ground. The eggs are deposited near the base of the tree. Larvae bore into and feed in the heartwood for three to four years (Drooz 1985). *Urographis fasciatus* (DeGeer) is a common eastern U. S. species whose larvae feed in hardwoods, such as oak, and also pine (Lingafelter 2007). *Xylotrechus sagittatus sagittatus* (Germar) breeds in dead conifers and is common in the eastern United States. It is attracted to logs, slash, fire-killed and bark beetle-killed trees (Drooz 1985).

Table 4.1. Temporal distribution of six species of Cerambycidae. Species occurred in the listed weeks of decay during season 1 / season 2.

Species	**Host**	**Season 1**	**Season 2**	**Total**	**Decay Week**
Acanthocinus nodosus (F.)	Pine	0	1	**1**	/ 4
Asemum striatum (L.)	Pine	0	13	**13**	/ 1, 2, 3
Cyrtinus pygmaeus (Halderman)	Oak	0	1	**1**	/ 1
Stenodontes dasytomus dasytomus (Say)	Oak	0	2	**2**	/ 16
Urographis fasciatus (DeGeer)	Oak	0	3	**3**	/ 2, 3, 8
Xylotrechus sagittatus sagittatus (Germar)	Pine	1	2	**3**	1 / 1, 2

4.4.3 Corylophidae: *Arthrolips fasciata* (Erichson)

One female specimen (Appendix G, Figure 7) was collected during season 2 on May 2, 2005, four weeks after the host loblolly pine was felled. It was collected at site 5 from bolt A, section 4. This species was first described from Tanzania and was subsequently collected from Australia, New South Wales, New Zealand, France (Bowestead 2003; Dauphin 2004), Italy (Ratti 2007), Taiwan, and for the first time in North America, Florida (Thomas 2005). Louisiana is the second state known to harbor this species and represents the most western distribution known in the U. S. Presence in the Feliciana Preserve may represent a recent range extension or may simply be a further indication of the type of habitats that need to be explored to discover such unique, minute beetles. The majority of published specimens were associated with pine needles.

4.4.4 Cucujidae: *Pediacus subglaber* LeConte

These beetles are ~5mm, elongate, parallel-sided, and dorsoventrally flattened. Unlike other cucujids, the temples are absent or represented at most by a small denticle. Six of the seven North American *Pediacus* species are distributed in the west, and *P. subglaber* (Appendix G, Figure 8) is the only species found in the east south of New England (Thomas 2004). This represents a new state record for Louisiana.

4.4.5 Curculionidae: *Ips* spp.

These three species (Table 4.2) are quite common in the southeast and breed in many *Pinus* trees. *Ips avulsus* (Eichhoff) is the smallest of the genus. It usually attacks the tops and limbs of trees, especially freshly cut trees. *Ips calligraphus* (Germar) attacks trunks, stumps and large limbs of recently felled trees. *Ips grandicollis* (Eichhoff) attacks recently felled trees and slash. Trunks and limbs are preferred only if other infestations occur (Drooz 1985). Specimens of *Ips* were lower in abundance than expected and likely limited given the rapid loss of moisture in sections of the bolts.

Table 4.2. Temporal distribution of six species of Curculiondae: *Ips* spp. Species occurred in the listed weeks of decay during season 1 / season 2.

Species	**Host**	**Season 1**	**Season 2**	**Total**	**DecayWeek**
Ips avulsus (Eichhoff)	Pine, Oak	4		**4**	3, 12, 16 /
Ips calligraphus (Germar)	Pine		1	**1**	/ 2
Ips grandicollis (Eichhoff)	Pine	1	8	**9**	8 / 1, 2, 3, 8, 12

4.4.6 Elateridae: *Drapetes quadripustulatus* Bonvouloir

Distinguishing characteristics include total length ~4mm, serrate antennae, simple claws, tarsomeres 1-4 with membranous ventral lobes, black prothorax, and black elytra each with a pair of red spots. This species (Appendix G, Figure 9) is reported from Texas, Wisconsin, Maryland, and Florida (Thomas 1995). My research has documented it as a new state record for Louisiana.

4.4.7 Endomychidae: *Micropsephodes lundgreni* Leschen and Carlton

Known distribution of this minute (1-1.2mm) spherical handsome fungus beetle (Appendix G, Figure 11) includes FL, LA, and TN. Leschen and Carlton (2000) recently described the species as the first representative of a mainly neotropical genus. The 24 specimens from southern red oak and 4 from loblolly pine at the Feliciana Preserve add to the few specimens previously collected in Louisiana.

CHAPTER 5: CONCLUSIONS

5.1 Conclusions and Summary

As a dying tree decays, overlapping successions of insects invade according to the species of tree and the stage of decomposition. The purpose of this research was to document beetle succession of felled loblolly pines and southern red oaks by determining which species of beetles colonize cut, reassembled, and standing bolts of pine and oak, and discovering the sequence of each beetle species' arrival. Twelve trees of each species located among a total of six sites in the Feliciana Preserve were studied during two seasons: late fall and mid spring. Species richness was indeed significantly higher on oak as hypothesized but pine was not higher in species abundance.

Southern red oak taxa were more similar between consecutive weeks of decays and thus succession was more gradual, as hypothesized, compared to loblolly pine taxa. As expected, significant differences in the week to week colonization of trunks were detected for all five beetle assemblages that completed analysis, both between the two tree species and the two seasons in which trees were felled. Higher quality substrate hardwood versus softwood and the ability to retain more moisture and thus support a wide array of micro-organisms explain the disparity in species abundance, richness, and succession patterns between the southern red oak and loblolly pine bolts sampled and analyzed. Seasonal differences in succession patterns are possibly explained by a combination of phloem availability, temperature, relative humidity, and other environmental condition.

Although not statistically analyzed, life histories of the beetle families, especially with regard to feeding guilds, likely influenced the trends seen in succession of beetle assemblages. Staphylinidae are known to be predators, fungivores and detritivores. Zopherids and Histerids also prey on other organisms and consume fungi but some Histeridae are also inquilinous (associated and often integrated into social insect colonies). Two specimens of *Terapus* n. sp. (Histeridae; Figure G.12) were collected from among *Pheidole* colonies in bolts. Curculionidae were also diverse; feeding habits include fungivores, phloeom-feeders, and ambrosial fungi consumers.

Although statistical differences were detected, succession studies usually require decades to be an effective predictive model. This study shows that even small scale studies (N=24 trees) can yield useful information if care is taken to standardize the sampling regime and take into account all possible confounding factors in the model (*e.g.,* including the first-order autoregressive option as an effect in the error term to account for repeated measures in time). Continuous improvement of small scale studies may lead to even greater *biological* significance of results.

Previous work on standing dead trees used passive traps such as emergence and sticky traps to collect insects. The study design employed here targets the species that are actually occupying the sampled tree. My results have increased the number of species known to inhabit recently dead loblolly pine and southern red oak, two economically important tree species. This study has demonstrated the existence of a rich saproxylic beetle fauna in standing bolts of loblolly pine and southern red oak at an early stage of decay (initial six months) and has provided novel and baseline information about saproxylic beetle succession patterns in south Louisiana forest habitats.

5.2 Future Research

Future research can supplement the inventory of ecological patterns among saproxylic coleopteran represented in this project by use of additional sampling methods, tree felling months, increased size of bolts, and varying forest habitats. Investigations into and, potentially, purposeful manipulation of the roles of fermentation, decay, and fungal growth products as well as emitted volatiles may shed more light on the underlying properties causing these two tree types to entice or dispel visiting organisms. Also, studies that can record simultaneous colonization habits of all arthropods, especially the aforementioned Formicidae and Isoptera, fungi, and other saproxylic microorganisms, will have a better understanding of how disturbance and succession operate. Further comparable and multi-year studies are needed to estimate succession patterns comprehensively for different forest types and to supplement investigations into the importance of coarse woody debris in forests.

REFERENCES CITED

Abrahamsson, M. and M. Lindbladh. 2006. A Comparison of Saproxylic Beetle Occurrence Between Man-Made High- And Low-Stumps of Spruce. Forest Ecology and Management. 226: 230-237.

ACITS. 1995. Factor Analysis Using SAS PROC FACTOR. Usage Note: Stat-53. Copyright 1995-1997, ACITS, The University of Texas at Austin Statistical Services. Available at: http://www.utexas.edu/cc/docs/stat53.html. Accessed November 24, 2007.

Arnett, R. H., Jr., and M. C. Thomas. 2001. American Beetles Volume 1. CRC Press LLC, Boca Raton, FL. 443 pp.

Arnett, R. H., Jr., M. C. Thomas, P E. Skelley, and J. H. Frank. 2002. American Beetles Volume 2. CRC Press LLC, Boca Raton, FL. 861 pp.

Avery, T. E. 1975. Natural Resources Measurements. McGraw-Hill, New York, NY. Second Edition. 339 pp.

Bengtson, S. 2005. Coleoptera. Lunds University's Museum of Entomology. Available at: http://www.biomus.lu.se/zoomus/ZooDoc/VetSam/ZooEnt/OrdCol/ListCol/008CarabidaeI.html. Accessed on December 10, 2005.

Berisford, C. W. 1980. Natural Enemies and Associated Organisms. Chapter 3 *In*: Thatcher, R.C., J.L. Searcy, J.E. Coster and G.B. Hertel (eds.). The southern Pine Beetle. USDA Technical Bulletin 1631: 31-52.

Blackman, M. W., and H. H. Stage. 1924. On the Succession of Insects Living in the Bark and Wood of Dying, Dead, and Decaying Hickory. NY State College of Forestry, Syracuse, NY. Technical Publication 17: 3-269.

Borden, J.H., Ryker, L.C., Chong, L.J., Pierce, H.D., Johnston, B.D. and A.C. Oehlschlager. 1987. Response of the Mountain Pine-Beetle, *Dendroctonus-ponderosae* Hopkins (Coleoptera-Scolytidae), to 5 Semiochemicals in British-Columbia Lodgepole Pine Forests. Canadian Journal of Forest Research. 17: 118-128.

Bowestead, S. 2003. Contribution to the Knowledge of the Corylophidae Of The Palaearctic Region (Coleoptera). *In*: Cuccodoro G. & Leschen R.A.B. (Eds.), Systematics of Coleoptera: Papers celebrating the retirement of Ivan Lobl. Memoirs on Entomology, International, 17, 2003, V+955 pp.

Calder, A. A. 2002. Group: ADEPHAGA. Australian Faunal Directory Checklist Output. Available at: http://www.deh.gov.au/cgi-bin/abrs/fauna/tree.pl?pstrVol=ADEPHAGA&pintMode=1. Accessed on December 10, 2005.

Camors, F. B., Jr., and T. L. Payne. 1972. Response of *Heydenia unica* (Hymenoptera: Pteromalidae) to *Dendroctonus frontalis* (Coleoptera: Scolytidae) Pheromones and a

Host-tree Terpene. Annals of the Entomological Society of America. 65: 31-33.

Carlton, C. E. D. S. Chandler, R. A. B. Leschen, E. G. Riley, and P. E. Skelley. 2005. Obituary and Dedication: Karl Heinz Stephan 1931-2005. The Coleopterists Bulletin. 59(3): 277–283.

Choate, P. M. 2001. An Asian ground beetle, *Mochtherus tetraspilotus* (MacLeay), in Florida (Coleoptera: Carabidae: Lebiini). Entomology Circular No. 404, Fla. Dept. Agric. & Consumer Services, Division of Plant Industry, Gainesville, FL. 2 pp.

Colwell, R. K. 2005. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8.0. User's Guide and application published at: http://purl.oclc.org/estimates.

Conners, P. 2007. Voices from the Past 40: February 1, 1905. Available at: http://www.fs.fed.us/r5/stanislaus/heritage/voices/voices40.shtml. Accessed on January 19, 2008.

Coulson, R. N. 1979. Population Dynamics of Bark Beetles. Annual Review of Entomology. 24: 417-447.

Cronin, J. T., J. L. Hayes, and P. Turchin. 2000. Evaluation of Traps Used to Monitor Southern Pine Beetle Aerial Populations and Sex Ratios. Agricultural and Forest Entomology. 2: 69-76.

Darlington, P. J., Jr. 1968. The Carabid Beetles of New Guinea Part III. Harpalinae (Continued): Perigonini to Pseudomorphini. Bulletin Museum Comparative Zoology. 137: 1-253.

Dauphin, P. 2004. Sur la présence en Gironde d'*Arthrolips fasciata* (Coleoptera Corylophidae). Bull. Soc. Linn. Bordeaux. 32: 147-148.

Delcourt, H. R. and P. A. Delcourt. 1974. Primeval Magnolia-Holly-Beech Climax in Louisiana. Ecology. 55: 638-644.

Delcourt, H. R. and P. A. Delcourt. 1975. The Blufflands: Pleistocene Pathway into the Tunica Hills. The American Midland Naturalist. 94(2): 385-400.

Drooz, A. T. (ed.) 1985. Insects of Eastern Forests. U.S. Department of Agriculture, Forest Service, Washington, D.C. Miscellaneous Publication 1426. 608 pp.

Dunn, J. P., and P. L. Lorio. 1992. Effects of Bark Girdling on Carbohydrate Supply and Resistance of Loblolly-Pine to Southern Pine-Beetle (*Dendroctonus-frontalis* Zimm) Attack. Forest Ecology and Management. 50: 317-330.

Edmonds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, Boston, MA. 630 pp.

FAO. 2000. U.N. Food and Agriculture Organization Forest Resources Assessment 2000. Available at: ftp://ftp.fao.org/docrep/fao/003/Y1997E/FRA%202000% 20Main%20 report.pdf. Accessed on March 12, 2005.

Ferrell, G.T. 1971. Host Selection by the Fir Engraver, *Scolytus ventralis* (Coleoptera: Scolytidae): Preliminary field studies. The Canadian Entomologist. 103: 1717-1725.

Gaumer, G. C., and R. I. Gara. 1967. Effects of Phloem Temperature and Moisture Content on Development of the Southern Pine Beetle. Contributions from Boyce Thompson Institute. 23: 373-377.

Gladstone, W.T., and F. T. Ledig. 1990. Reducing Pressure on Natural Forests through High-Yield Forestry. Forest Ecology and Management. 35: 69-78.

Graham, S. A. 1925. The Felled Tree Trunk as an Ecological Unit. Ecology. 6: 397-411.

Gutierrez, L. T., and W. R. Fey. 1980. Ecosystem Succession: A General Hypothesis and a Test Model of a Grassland. MIT Press, Cambridge, MA. 231 pp.

Habu, A. 1967. Fauna Japonica. Carabidae. Truncatipennes Group. (Insecta: Coleoptera). Biogeographical Society of Japan. Tokyo Electrical Engineering College Press, pub. 338 p. 27pls.

Hanula, J. L. 1996. Relationship of Wood-Feeding Insects and Coarse Woody Debris. *In*: McMinn, J.W., Crossley Jr., D.A. (Eds.), Biodiversity and Coarse Woody Debris in Southern Forests, Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. Gen. Tech. Rep. SE-94 Asheville, NC: USDA Forest Service, Southern Research Station.

Hanula, J. L. and K. Franzreb. 1998. Source, Distribution and Abundance of Macroinvertebrates on the Bark of Longleaf Pine: Potential Prey of Red-cockaded Woodpecker. Forest Ecology and Management. 102: 89-102.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack Jr., and K. W. Cummins. 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. Advances in Ecological Research. 15: 133-302.

Hines, J. W., and H. J. Heikkenen. 1977. Beetles Attracted to Severed Virginia Pine (*Pinus virginiana* Mill.). Environmental Entomology. 6: 123-127.

Howden, H. F., and G. B. Vogt. 1951. Insect Communities of Standing Dead Pine (*Pinus virginiana* Mill.). Annals of the Entomological Society of America. 44: 581-595.

Jedlicka, A. 1963. Monographie der Truncatipennen aus Ostasien. Lebiinae - Odacanthinae - Brachyninae. (Coleoptera, Carabidae). Entomologische Abhandlungen und berichte aus dem Staatl., Museum für Tierkunde in Dresden. 28: 269-368.

Kaila, L., P. Martikainen, and P. Puntilla. 1997. Dead Trees Left in Clear-Cuts Benefit Saproxylic Coleoptera Adapted to Natural Disturbances in Boreal Forest. Biodiversity and Conservation. 6: 1-18.

Leschen, R. A. B., and C. E. Carlton. 2000. A New Species of *Micropsephodes* from Southern United States (Coleoptera: Endomychidae: Anamorphinae). Coleopterists Bulletin. 54: 232-238.

Landau, D., D. Prowell, and C. Carlton. 1999. Intensive Versus Longterm Sampling to Assess Lepidopteran Diversity in a Southern Mixed Mesophytic Forest. Annals of the Entomological Society of America. 92: 435-441.

Lingafelter, S. W. 2007. Illustrated Key to the Longhorned Woodboring Beetles of the Eastern United States. The Coleopterists Bulletin. Special Publication No. 3. North Potomac, MD. 208pp.

Majer, J. D., Recher, H. F., Graham, R., and R. Gupta. 2003. Trunk Invertebrate Faunas of Western Australian Forests and Woodlands: Influence of Tree Species and Season. Austral Ecology. 28: 629–641.

Raffa, K.F. and A. A. Berryman. 1983. The Role of Host Plant Resistance in the Colonization Behavior and Ecology of Bark Beetles (Coleoptera, Scolytidae). Ecological Monographs. 53: 27-49.

Raffa, K. F., Phillips, T. W., and S. M. Salom. 1993. Strategies and Mechanisms of Host Colonization by Bark Beetles. *In*: Schowalter, T. D. and G. M. Filip (Eds.). Beetle Pathogen Interactions in Conifer Forest. Academic Press, London. 252 pp.

Ratti, E. 2007. Biodiversità della Laguna Di Venezia e della Costa Nord Adriatica Veneta. Segnalazioni 193. Boll. Mus. civ. St. Nat. Venezia. 58: 319-328.

Renwick, J. A. A., and J. P. Vité. 1969. Bark Beetle Attractants: Mechanism of Colonization by *Dendroctonus frontalis*. Nature. 224: 1222-1223.

Riley, M. A. M. 1983. Insect Enemies of *Ips calligraphus* (Germar) on Felled loblolly (*Pinus taeda* L.) and Slash (*P. elliottii* Englemann) Pines in Louisiana. Master's Thesis, Louisiana State University. USA. 94 pp.

Savely, H. E. 1939. Ecological relations of certain animals in dead pine and oak logs. Ecological Monographs. 9: 323-385.

Schoenly, K. and W. Reid. 1987. Dynamics of heterotrophic succession in carrion arthropod assemblages: Discrete seres or a continuum of change? Oecologia. 73 (2): 192-202.

Shelford, V.E. 1913. Animal Communities in Temperate America as Illustrated in the Chicago Region. Bulletin No. 5, Geographical Society of Chicago, IL. 362 pp.

Speight, M. C. D. 1989. Saproxylic Invertebrates and their Conservation. Council of Europe.

Nature and Environment Series 42, Strasbourg. 82 pp.

Stephan, K. H. 1989. The Bothrideridae and Colydiidae of America North of Mexico (Coleoptera: Clavicornia and Heteromera). Occasional Papers of the Florida State Collection of Arthropods. 6: 1-65.

Thatcher, R.C., J.L. Searcy, J.E. Coster and Gerald D. Hertel. 1980. The Southern Pine Beetle. USDA Forest Service Technical Bulletin 1631. 266 pp.

Thomas, M. C. 1995. Family Elateridae. A Distributional Checklist of the Beetles (Coleoptera) of Florida. Available at: http://www.fsca-dpi.org/Coleoptera/Mike/elater.htm. Accessed on December 10, 2005.

Thomas, M. C. 2004. A Revision of *Pediacus* Shuckard (Coleoptera: Cucujidae) for America North of Mexico, with Notes on other Species. Insecta Mundi. 17: 157-177.

Zhong, H. and T. D. Schowalter. 1989. Conifer Bole Utilization by Wood-boring Beetles in Western Oregon. Canadian Journal of Forest Research. 19: 943-947.

APPENDIX A: TAXA CHECKLIST

Table A.1. Complete list of 190 beetle taxa collected from freshly killed Loblolly Pine (“Pine”) and Southern Red Oak (“Oak”) trees during season 1 (in part, October 2004 - March 2005) and season 2 (April - September 2005) at the Feliciana Preserve, West Feliciana Parish, LA.

Family	Taxa	Host Tree	Season
Anthribidae	*Araecerus coffeae* (F.)	Pine	1
	Euparius marmoreus (Olivier)	Pine	1
Biphyllidae	*Diplocoelus rudis* (LeConte)	Pine, Oak	1, 2
Brentidae	*Arrhenodes minutus* (Drury)	Pine, Oak	2
Carabidae	*Clinidium baldufi* Bell	Pine, Oak	2
	Coptodera aerata Dejean	Oak	2
	Cymindis platicollis (Say)	Pine	1
	Mioptachys flavicauda (Say)	Pine, Oak	1, 2
	Mochtherus tetraspilotus (MacLeay)	Pine	1
	Omoglymmius americanus (Laporte)	Pine	1
	Perigona pallipennis (LeConte)	Oak	2
	Phloeoxena signata (Dejean)	Pine, Oak	1, 2
	Piesmus submarginatus (Say)	Pine, Oak	1, 2
	Polyderis laevis (Say)	Oak	2
Cerambycidae	*Acanthocinus nodosus* (F.)	Pine	2
	Asemum striatum (L.)	Pine	2
	Cyrtinus pygmaeus (Halderman)	Oak	2
	Stenodontes dasytomus dasytomus (Say)	Oak	2
	Urographis fasciatus (DeGeer)	Oak	2
	Xylotrechus sagittatus sagittatus (Germar)	Pine	1, 2
Ceratocanthidae	*Germarostes globosus* (Say)	Oak	2
Cerylonidae	*Cerylon unicolor* (Ziegler)	Pine, Oak	1, 2
	Hypodacne punctata LeConte	Pine, Oak	2
	Philothermus glabriculus (LeConte)	Pine, Oak	1, 2
Chrysomelidae	*Paria fragariae* Wilcox	Pine	2
Ciidae	*Cis creberrimus* Mellié	Pine, Oak	2
Coccinellidae	*Exochomus marginipennis* (LeConte)	Oak	2
Corylophidae	*Arthrolips fasciata* (Erichson)	Pine	2

Table A.1. continued

	Arthrolips splendens (Schwarz)	Pine	2
	Clypastraea specularis (Casey)	Oak	1, 2
Cucujidae	*Pediacus subglaber* LeConte	Pine, Oak	1, 2
Curculionidae	*Cossonus corticola* Say	Pine, Oak	1, 2
	Cossonus impressifrons Boheman	Pine, Oak	1, 2
	Cyrtepistomus castaneus (Roelofs)	Oak	2
	Dendroctonus terebrans (Olivier)	Pine	1
	Dryophthorus americanus Bedel	Pine, Oak	2
	Euplatypus compositus (Say)	Oak	1, 2
	Gnathotrichus materiarius (Fitch)	Pine	2
	Hylastes tenuis Eichhoff	Pine, Oak	1
	Hylobius pales (Herbst)	Pine	2
	Hypothenemus crudiae (Panzer)	Pine, Oak	1, 2
	Ips avulsus (Eichhoff)	Pine, Oak	1
	Ips calligraphus (Germar)	Pine	2
	Ips grandicollis (Eichhoff)	Pine	1, 2
	Monarthrum mali (Fitch)	Oak	1, 2
	Myoplatypus flavicornis (F.)	Pine	2
	Orthotomicus caelatus (Eichhoff)	Pine	1, 2
	Oxoplatypus quadridentatus (Olivier)	Oak	2
	Pachylobius picivorus (Germar)	Pine	2
	Pissodes nemorensis Germar	Pine	2
	Pityoborus comatus (Zimmermann)	Pine	2
	*Pseudopityophthorus pruinosu*s (Eichhoff)	Oak	2
	Rhyncolus discors Casey	Pine, Oak	1, 2
	Stenoscelis andersoni Buchanan	Oak	2
	Stenoscelis brevis (Boheman)	Pine, Oak	2
	Tomolips quercicola (Boheman)	Pine	2
	Xyleborinus saxeseni (Ratzeburg)	Pine, Oak	1, 2
	Xyleborus affinis Eichhoff	Pine, Oak	1, 2
	Xyleborus ferrugineus (F.)	Pine, Oak	1, 2
	Xyleborus pubescens Zimmermann	Pine, Oak	1, 2
	Xyleborus validus Eichhoff	Oak	1, 2
	Xylosandrus compactus (Eichhoff)	Pine	2

Table A.1. continued

	Xylosandrus crassiusculus (Motschulsky)	Pine, Oak	1, 2
Elateridae	*Alaus myops* (F.)	Pine	2
	Ampedus alabamensis Ramberg	Oak	1
	Melanotus morosus Candèze	Oak	1, 2
	Drapetes quadripustulatus Bonvouloir	Pine, Oak	2
Endomychidae	*Clemmus minor* Crotch	Pine, Oak	2
	Micropsephodes lundgreni Leschen & Carlton	Pine, Oak	1, 2
	Rhanidea unicolor (Ziegler)	Pine, Oak	1, 2
Eucnemidae	*Dirrhagofarsus lewisi* (Fleutiaux)	Oak	2
	Nematodes atropos (Say)	Oak	2
Histeridae	*Acritus exiguus* (Erichson)	Pine, Oak	2
	Aeletes floridae (Marseul)	Pine, Oak	1, 2
	Aeletes simplex (LeConte)	Pine, Oak	1, 2
	Bacanius punctiformis (LeConte)	Pine, Oak	2
	Eblisia carolina (Paykull)	Pine, Oak	2
	Epierus pulicarius (Erichson)	Pine, Oak	2
	Hololepta lucida (LeConte)	Oak	2
	Paromalus seminulum Erichson	Pine, Oak	1, 2
	Pinaxister setiger (LeConte)	Oak	2
	Platylomalus aequalis (Say)	Oak	2
	Platysoma coarctatum LeConte	Pine, Oak	1, 2
	Platysoma cylinidrica (Palisot)	Pine	2
	Platysoma lecontei Marseul	Pine, Oak	1, 2
	Platysoma parallela Say	Pine	1, 2
	Plegaderus barbelini Marseul	Pine	2
	Plegaderus transversus Say	Pine, Oak	1, 2
	Terapus n. sp.	Oak	2
Laemophloeidae	*Dysmerus basalis* Casey	Oak	2
	Laemophloeus biguttatus (Say)	Oak	2
	Laemophloeus megacephalus Grouvelle	Oak	1, 2
	Phloeolaemus chamaeropis (Schwarz)	Pine, Oak	1, 2
	Placonotus modestus (Say)	Oak	1
	Placonotus zimmermanni (LeConte)	Pine, Oak	1, 2
Lampyridae	*Photinus* sp.	Pine	2

Table A.1. continued

Latridiidae	*Enicmus maculatus* (LeConte)	Oak	2
Leiodidae	*Agathidium exiguum* Melsheimer	Pine, Oak	1, 2
Monotomidae	*Bactridium ephippigerum* (Guérin-Méneville)	Oak	1, 2
	Rhizophagus sayi Schaeffer	Oak	1
Mycetophagidae	*Litargus balteatus* LeConte	Pine, Oak	1, 2
	Mycetophagus pini Ziegler	Pine	1
Nitidulidae	*Carpophilus corticinus* Erichson	Pine, Oak	1, 2
	Carpophilus dimidiatus (F.)	Oak	1
	Carpophilus marginatus Erichson	Oak	1, 2
	Carpophilus tempestivus Erichson	Oak	1, 2
	Colopterus niger (Say)	Oak	1, 2
	Colopterus semitectus (Say)	Oak	1, 2
	Colopterus truncatus (Randall)	Pine, Oak	1, 2
	Colopterus unicolor (Say)	Pine, Oak	1, 2
	Cryptarcha ampla Erichson	Oak	2
	Epuraea erichsoni Reitter	Pine, Oak	1, 2
	Epuraea luteola Erichson	Oak	1
	Epuraea truncatella Mannerheim	Pine	1
	Prometopia sexmaculata (Say)	Oak	1, 2
	Stelidota geminata (Say)	Oak	1
Nosodendridae	*Nosodendron unicolor* Say	Oak	2
Passandridae	*Catogenus rufus* (F.)	Pine, Oak	2
Ptiliidae	Ptiliidae spp.	Pine, Oak	1, 2
Ptilodactylidae	*Ptilodactyla* sp.	Oak	2
Scymaenidae	*Connophron* sp.	Oak	2
	Microscydmus sp.	Oak	1
Silvanidae	*Ahasverus advena* (Waltl)	Pine, Oak	2
	Cathartosilvanus imbellis (LeConte)	Oak	2
	Silvanus muticus Sharp	Pine, Oak	1, 2
	Uleiota dubia (F.)	Oak	2
Staphylinidae	*Actiastes globiferum* (LeConte)	Oak	2
	Atheta sp.	Pine, Oak	1, 2
	Batrisodes clypeonotus (Brendel)	Oak	1
	Batrisodes uncicornis Casey	Oak	1

Table A.1. continued

	Belonuchus rufipennis (F.)	Pine	1, 2
	Clavilispinus rufescens (LeConte)	Pine, Oak	1, 2
	Coproporus ventriculus (Say)	Pine, Oak	1, 2
	nr. *Cyphea* sp.	Pine, Oak	1, 2
	Dianusa sp.	Pine, Oak	1, 2
	Holobus sp.	Oak	1, 2
	Homalota sp.	Pine	2
	Homalotini, not *Dianusa*	Pine	2
	Laetulonthus laetulus (Say)	Pine, Oak	1, 2
	Leptusa spp.	Pine, Oak	1, 2
	Lordithon obsoletus (Say)	Oak	1
	Myrmecocephalus cingulatus (LeConte)	Pine	2
	Myrmecocephalus concinnus (Erichson)	Pine, Oak	1, 2
	Nacaeus tenuis (LeConte)	Oak	1
	Nudobius cephalus (Say)	Pine, Oak	1, 2
	prob. *"Omalium" fractum* Fauvel	Pine, Oak	1
	Oxybleptes davisi (Notman)	Oak	1, 2
	Paederinae nr. *Medon*	Oak	2
	Placusa sp.	Pine, Oak	1, 2
	Platydracus sp.	Pine	1
	Sepedophilus cinctulus (Erichson)	Pine, Oak	1, 2
	Sepedophilus littoreus (L.)	Oak	2
	Sepedophilus scriptus (Horn)	Pine	2
	Silusa sp.	Pine	1
	Thoracophorus costalis (Erichson)	Pine, Oak	1, 2
	Tmesiphorus carinatus (Say)	Pine, Oak	2
	Trichopsenius xenoflavipes Seevers	Pine, Oak	2
Tenebrionidae	*Alobates pennsylvanicus* (DeGeer)	Pine, Oak	2
	Corticeus glaber (LeConte)	Pine	2
	Corticeus thoracicus (Melsheimer)	Pine, Oak	1, 2
	Gnatocerus guatemalensis (Champion)	Oak	2
	Isomira pulla (Melsheimer)	Oak	2
	Platydema flavipes (F.)	Pine	1, 2
	Platydema laevipes Haldeman	Oak	2

Table A.1. continued

	Platydema ruficorne (Sturm)	Pine	1
	Statira liebecki Leng	Pine	2
Tetratomidae	*Eustrophopsis bicolor* (F.)	Pine	1
	Eustrophus tomentosus Say	Oak	1
Trogossitidae	*Corticotomus depressus* Schaeffer	Oak	2
	Temnochila virescens (F.)	Pine	2
	Tenebroides americanus (Kirby)	Oak	1, 2
	Tenebroides corticalis (Melsheimer)	Pine, Oak	1, 2
	Tenebroides nanus (Melsheimer)	Oak	2
	Tenebroides obtusus (Horn)	Oak	2
Zopheridae	*Aulonium parallelopipedum* (Say)	Oak	2
	Aulonium tuberculatum LeConte	Pine	2
	Bitoma carinata (LeConte)	Pine, Oak	1, 2
	Bitoma quadricollis (Horn)	Pine, Oak	1, 2
	Colydium lineola Say	Pine, Oak	1, 2
	Endeitoma granulata (Say)	Pine	2
	Eucicones marginalis (Melsheimer)	Oak	2
	Lasconotus referendarius Zimmermann	Pine, Oak	1, 2
	Microsicus parvulus Guerin-Meneville	Oak	1, 2
	Namunaria guttulata (LeConte)	Pine, Oak	1, 2
	Nematidium filiforme LeConte	Oak	2
	Paha laticollis (LeConte)	Pine	1
	Pycnomerus haematodes (F.)	Pine, Oak	1, 2
	Pycnomerus reflexus Say	Pine, Oak	1, 2
	Pycnomerus sulcicollis LeConte	Pine, Oak	2
	Synchita fuliginosa Melsheimer	Oak	2

APPENDIX B: THIRTY MOST ABUNDANT TAXA BY SEASON AND HOST TREE

Table B.1. This dataset of the 30 most abundant beetle taxa accounts for 96.5 % of all specimens (49,320/51,119) and was used for multivariate and regression analyses after being log (x+1) transformed. Frequency data listed include the season and host tree species. Season 1 (in part) = October 2004 March 2005; Season 2 = April - September 2005; Pine = Loblolly Pine; Oak = Southern Red Oak

		Season 1			Season 2			
Family	**Taxa**	**Pine**	**Oak**	**Total**	**Pine**	**Oak**	**Total**	**Totals**
Carabidae	*Mioptachys flavicauda*	6	6	12	543	530	1073	**1085**
Cerylonidae	*Cerylon unicolor*	2	8	10	170	347	517	**527**
Curculionidae	*Cossonus corticola*	140	5	145	2877	2	2879	**3024**
	Cossonus impressifrons	0	3	3	8	1560	1568	**1571**
	Xyleborinus saxeseni	9	2	11	211	24	235	**246**
	Xyleborus affinis	1	35	36	5	90	95	**131**
Histeridae	*Aeletes floridae*	369	3847	4216	544	4072	4616	**8832**
	Bacanius punctiformis	0	0	0	13	352	365	**365**
	Platysoma coarctatum	19	30	49	28	7	35	**84**
	Platysoma lecontei	2	54	56	13	133	146	**202**
	Platysoma parallela	3	0	3	119	0	119	**122**
	Plegaderus transversus	0	1	1	316	0	316	**317**
Laemophloeidae	*Phloeolaemus chamaeropis*	0	216	216	1	703	704	**920**
Nitidulidae	*Carpophilus corticinus*	95	249	344	26	88	114	**458**
	Carpophilus tempestivus	0	229	229	0	511	511	**740**
	Colopterus niger	0	464	464	0	403	403	**867**
	Colopterus semitectus	0	12	12	0	246	246	**258**

Table B.1. continued

	Colopterus truncatus	4	157	161	0	203	203	**364**
	Epuraea erichsoni	8	213	221	1	18	19	**240**
Ptiliidae	Ptiliidae spp.	0	1	1	258	772	1030	**1031**
Silvanidae	*Silvanus muticus*	820	502	1322	956	1638	2594	**3916**
Staphylinidae	*Laetulonthus laetulus*	2	14	16	14	90	104	**120**
	Leptusa spp.	17	43	60	47	5	52	**112**
	Myrmecocephalus concinnus	219	464	683	92	334	426	**1109**
	Placusa sp.	689	11250	11939	476	8010	8486	**20425**
	Thoracophorus costalis	0	11	11	31	102	133	**144**
Tenebrionidae	*Corticeus glaber*	0	0	0	204	0	204	**204**
Zopheridae	*Bitoma quadricollis*	0	75	75	1	53	54	**129**
	Pycnomerus haematodes	1	0	1	76	15	91	**92**
	Pycnomerus reflexus	0	6	6	136	1543	1679	**1685**
	Totals	**2406**	**17897**	**20303**	**7166**	**21851**	**29017**	**49320**

APPENDIX C: THIRTY MOST ABUNDANT TAXA BY SEASON AND DECAY WEEK

Table C.1. Season 1 (in part, October 2004 - March 2005) frequency data for the 30 most abundant beetle taxa include the decay week (number of weeks since trees were felled) and sampling date. This dataset was used for succession graphs and, after being log (x+1) transformed, multivariate and regression analyses. (N = 20,303)

		Week 1	Week 2	Week 3	Week 4	Week 8	Week 12	Week 16	Week 20	Week 24	
		11-Oct	**18-Oct**	**25-Oct**	**1-Nov**	**29-Nov**	**27-Dec**	**24-Jan**	**21-Feb**	**21-Mar**	**Total**
Carabidae	*Mioptachys flavicauda*	1	1	2	4	0	1	1	1	1	**12**
Cerylonidae	*Cerylon unicolor*	0	0	1	0	1	1	3	1	3	**10**
Curculionidae	*Cossonus corticola*	2	11	59	62	6	3	1	1	0	**145**
	Cossonus impressifrons	0	0	0	0	0	0	0	2	1	**3**
	Xyleborinus saxeseni	3	2	2	2	0	1	0	1	0	**11**
	Xyleborus affinis	26	6	2	1	0	0	1	0	0	**36**
Histeridae	*Aeletes floridae*	247	331	303	201	156	197	577	1254	950	**4216**
	Bacanius punctiformis	0	0	0	0	0	0	0	0	0	**0**
	Platysoma coarctatum	0	4	13	13	3	1	0	11	4	**49**
	Platysoma lecontei	2	0	4	4	0	0	11	15	20	**56**
	Platysoma parallela	0	0	1	1	1	0	0	0	0	**3**
	Plegaderus transversus	0	0	0	0	0	0	1	0	0	**1**
Laemophloeidae	*Phloeolaemus chamaeropis*	13	49	78	28	5	17	18	6	2	**216**
Nitidulidae	*Carpophilus corticinus*	67	121	88	51	5	5	5	2	0	**344**
	Carpophilus tempestivus	52	86	68	14	1	0	3	5	0	**229**
	Colopterus niger	113	148	113	80	4	1	2	3	0	**464**
	Colopterus semitectus	7	2	2	0	0	0	0	0	1	**12**
	Colopterus truncatus	94	43	24	0	0	0	0	0	0	**161**
	Epuraea erichsoni	52	88	59	18	2	2	0	0	0	**221**
Ptiliidae	Ptiliidae spp.	0	0	0	1	0	0	0	0	0	**1**

Table C.1. continued

Silvanidae	*Silvanus muticus*	67	98	82	48	404	289	127	87	120	**1322**
Staphylinidae	*Laetulonthus laetulus*	3	0	4	7	1	0	0	1	0	**16**
	Leptusa spp.	0	1	0	1	2	2	8	32	14	**60**
	Myrmecocephalus concinnus	137	106	59	55	138	58	70	38	22	**683**
	Placusa sp.	3088	2371	2873	1957	967	323	277	50	33	**11939**
	Thoracophorus costalis	0	1	1	4	2	2	0	1	0	**11**
Tenebrionidae	*Corticeus glaber*	0	0	0	0	0	0	0	0	0	**0**
Zopheridae	*Bitoma quadricollis*	0	0	0	0	2	1	55	17	0	**75**
	Pycnomerus haematodes	0	0	0	0	0	1	0	0	0	**1**
	Pycnomerus reflexus	0	0	1	2	1	0	1	0	1	**6**
	Totals	**3974**	**3469**	**3839**	**2554**	**1701**	**905**	**1161**	**1528**	**1172**	**20303**

Table C.2. Season 2 (April - September 2005) frequency data for the 30 most abundant beetle taxa include the decay week (number of weeks since trees were felled) and sampling date. This dataset was used for succession graphs and, after being log (x+1) transformed, multivariate and regression analyses. (N = 29,017)

		Week 1	**Week 2**	**Week 3**	**Week 4**	**Week 8**	**Week 12**	**Week 16**	**Week 20**	**Week 24**	
		11-Apr	18-Apr	25-Apr	2-May	30-May	27-Jun	25-Jul	22-Aug	19-Sep	**Total**
Carabidae	*Mioptachys flavicauda*	5	11	23	9	57	97	228	236	407	**1073**
Cerylonidae	*Cerylon unicolor*	3	8	20	18	60	108	112	113	75	**517**
Curculionidae	*Cossonus corticola*	0	9	78	400	1901	334	117	18	22	**2879**
	Cossonus impressifrons	0	0	0	0	328	986	236	16	2	**1568**
	Xyleborinus saxeseni	16	66	97	47	8	1	0	0	0	**235**
	Xyleborus affinis	0	74	17	4	0	0	0	0	0	**95**
Histeridae	*Aeletes floridae*	587	712	292	378	1345	982	259	59	2	**4616**
	Bacanius punctiformis	0	0	1	0	89	131	53	44	47	**365**
	Platysoma coarctatum	0	9	2	4	10	9	1	0	0	**35**

Table C.1. continued

	Platysoma lecontei	15	9	22	20	24	29	11	10	6	**146**
	Platysoma parallela	0	14	57	42	2	4	0	0	0	**119**
	Plegaderus transversus	0	1	5	76	233	1	0	0	0	**316**
Laemophloeidae	*Phloeolaemus chamaeropis*	68	236	220	142	33	3	1	1	0	**704**
Nitidulidae	*Carpophilus corticinus*	37	34	22	18	3	0	0	0	0	**114**
	Carpophilus tempestivus	264	168	75	4	0	0	0	0	0	**511**
	Colopterus niger	135	139	113	15	1	0	0	0	0	**403**
	Colopterus semitectus	146	82	18	0	0	0	0	0	0	**246**
	Colopterus truncatus	136	59	8	0	0	0	0	0	0	**203**
	Epuraea erichsoni	9	8	1	1	0	0	0	0	0	**19**
Ptiliidae	Ptiliidae spp.	0	0	1	0	148	165	242	433	41	**1030**
Silvanidae	*Silvanus muticus*	452	507	385	238	294	399	171	120	28	**2594**
Staphylinidae	*Laetulonthus laetulus*	27	49	19	9	0	0	0	0	0	**104**
	Leptusa spp.	0	2	9	36	5	0	0	0	0	**52**
	Myrmecocephalus concinnus	39	130	74	115	18	49	1	0	0	**426**
	Placusa sp.	3119	3117	1639	568	32	11	0	0	0	**8486**
	Thoracophorus costalis	5	3	7	11	15	17	9	26	40	**133**
Tenebrionidae	*Corticeus glaber*	0	27	124	47	3	2	1	0	0	**204**
Zopheridae	*Bitoma quadricollis*	0	4	22	12	12	3	1	0	0	**54**
	Pycnomerus haematodes	0	0	0	1	1	4	9	31	45	**91**
	Pycnomerus reflexus	2	20	41	51	218	232	420	395	300	**1679**
	Totals	**5065**	**5498**	**3392**	**2266**	**4840**	**3567**	**1872**	**1502**	**1015**	**29017**

APPENDIX D: PRINCIPAL COMPONENT ANALYSIS

Table D.1. Factor loadings resulting from Varimax rotation. Using frequency data for the 30 most abundant beetle taxa, eight factors were extracted in the FACTOR procedure. Factor loadings, or correlations, greater than |0.30| (in bold) were considered significant and used to determine which taxa contributed to variation of each factor.

Family	Taxa	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
Carabidae	*Mioptachys flavicauda*	**0.61243**	0.01126	-0.05123	-0.09457	-0.00126	0.04823	**-0.33835**	-0.05664
Cerylonidae	*Cerylon unicolor*	**0.64665**	-0.02257	0.02149	-0.03043	-0.00225	0.07677	-0.02036	-0.03167
Curculionidae	*Cossonus corticola*	0.00589	-0.05316	-0.00981	-0.08449	0.08268	**0.84841**	-0.0966	-0.03639
Curculionidae	*Cossonus impressifrons*	**0.55645**	-0.13297	0.03312	-0.01518	-0.02595	-0.09565	**0.50412**	0.00779
Curculionidae	*Xyleborinus saxeseni*	-0.05629	0.0565	-0.02714	-0.03919	**0.60246**	-0.03947	-0.01071	0.03714
Curculionidae	*Xyleborus affinis*	0.01486	0.17465	**0.49255**	0.14775	0.01837	-0.01532	-0.16884	0.02569
Histeridae	*Aeletes floridae*	0.1996	0.06918	**0.47848**	0.08857	-0.01969	-0.03767	**0.5497**	0.2098
Histeridae	*Bacanius punctiformis*	**0.67323**	-0.05619	-0.02392	0.03124	-0.00825	-0.04837	0.27431	-0.08129
Histeridae	*Platysoma coarctatum*	-0.02093	0.04161	-0.13264	0.17075	-0.05783	0.22896	0.12505	**0.4612**
Histeridae	*Platysoma lecontei*	0.13437	0.11181	0.01992	-0.11049	-0.02114	-0.0762	**0.4504**	0.14074
Histeridae	*Platysoma parallela*	-0.01839	-0.04465	0.02503	-0.00451	**0.73775**	0.14442	-0.00206	0.00204
Histeridae	*Plegaderus transversus*	0.01736	-0.01814	0.01387	-0.00514	0.10275	**0.83825**	0.01121	0.12731
Laemophloeidae	*Phloeolaemus chamaeropis*	-0.0184	0.29145	**0.6504**	0.10388	-0.08884	-0.04863	0.04031	0.11123
Nitidulidae	*Carpophilus corticinus*	-0.07193	0.16704	0.11665	**0.63947**	-0.0291	-0.02134	-0.01844	0.00447
Nitidulidae	*Carpophilus tempestivus*	-0.03353	**0.72341**	**0.38104**	0.15088	-0.0361	-0.018	0.05039	0.02727
Nitidulidae	*Colopterus niger*	-0.03434	**0.56939**	0.29332	**0.39989**	-0.0437	-0.02331	-0.00195	0.03272
Nitidulidae	*Colopterus semitectus*	-0.01595	**0.73451**	0.18314	-0.13082	0.01396	0.000	0.08362	-0.01535
Nitidulidae	*Colopterus truncatus*	-0.03072	**0.65428**	-0.05042	0.26808	0.01073	-0.03349	0.0462	-0.06436
Nitidulidae	*Epuraea erichsoni*	-0.00724	0.10654	0.03718	**0.77321**	-0.00426	-0.02432	-0.05008	-0.00086
Ptiliidae	Ptiliidae spp.	**0.60733**	0.00355	-0.11383	0.0221	-0.08052	0.22824	0.06448	-0.02034
Silvanidae	*Silvanus muticus*	0.09903	0.09258	**0.54313**	-0.1174	0.17789	0.06272	**0.31746**	-0.15222

Table D.1. continued

Staphylinidae	*Laetulonthus laetulus*	-0.04189	0.22777	**0.44994**	-0.08529	0.0122	0.02208	-0.13499	-0.02188
Staphylinidae	*Leptusa* spp.	-0.02566	-0.00328	-0.08959	0.0219	**0.32076**	0.05842	0.04706	**0.60213**
Staphylinidae	*Myrmecocephalus concinnus*	-0.09583	-0.14928	**0.60777**	**0.37114**	-0.00491	-0.01962	0.13677	-0.03401
Staphylinidae	*Placusa* sp.	-0.19987	**0.49399**	**0.41627**	**0.45005**	-0.02008	-0.09775	0.07572	0.03104
Staphylinidae	*Thoracophorus costalis*	**0.33737**	0.05412	0.06722	-0.07711	-0.0008	-0.15064	-0.17281	0.22219
Tenebrionidae	*Corticeus glaber*	-0.01159	-0.05205	0.04619	0.00758	**0.7632**	0.06542	-0.00269	0.0014
Zopheridae	*Bitoma quadricollis*	-0.033	-0.08279	0.23624	-0.13654	-0.11089	-0.09142	-0.01539	**0.58867**
Zopheridae	*Pycnomerus haematodes*	0.21094	-0.05458	0.10535	-0.03759	-0.01103	-0.0479	**-0.49243**	0.08222
Zopheridae	*Pycnomerus reflexus*	**0.72935**	-0.05755	0.04355	-0.06411	-0.02685	-0.15064	0.02439	0.03677

Table D.2. Variance explained by each factor, before Varimax rotation. The eight extracted factors are ranked according to the greatest percentage of variation explained.

Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
4.14 %	2.85 %	1.97 %	1.51 %	1.29 %	1.22 %	1.10 %	1.04 %

Table D.3. Variance explained by each factor, after Varimax rotation of factor axes. The eight extracted factors are ranked according to the greatest percentage of variation explained.

Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
2.75 %	2.36 %	2.34 %	1.77 %	1.68 %	1.66 %	1.44 %	1.12 %

APPENDIX E: REGRESSION ANALYSIS

Type III tests of fixed effects and least squares means generated from the MIXED procedure. Factor scores (linear combinations of the factor loadings and all sample observations) were tested for significant differences among associated treatment effects. Tukey-Kramer values (P<0.05) assign different letters if comparisons of least squares means are significant. Factor scores 3, 4, and 8 could not complete analysis because of problems with infinite likelihood.

Table E.1. Class Level Information for each tested factor score

Class	Levels	Values
Season	2	1 2
Week	9	1 2 3 4 8 12 16 20 24
Site	6	1 2 3 4 5 6
TreeSp	2	Oak Pine
Dup	2	1 2
Bolt	3	A B C
Section	6	1 2 3 4 5 6

Table E.2. Factor Score 1: Type III Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Season	1	4	135.12	0.0003
TreeSp	1	4	36.98	0.0037
Season*TreeSp	1	4	27.12	0.0065
Bolt	2	46	2.63	0.0825
Section	5	355	2.32	0.0431
Week	8	3358	123.5	<.0001
Season*Week	8	3358	141.67	<.0001
Week*TreeSp	8	3358	40.47	<.0001
Season*Week*TreeSp	8	3358	52.67	<.0001

Table E.3. Factor Score 1: Least squares means

Effect	TreeSp	Bolt	Season	Week	Section	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
Season			2			0.4386	0.05356	4	8.19	0.0012	A
Season			1			-0.4425	0.05363	4	-8.25	0.0012	B
TreeSp	Oak					0.2285	0.05361	4	4.26	0.013	A
TreeSp	Pine					-0.2324	0.05358	4	-4.34	0.0123	B
Season*TreeSp	Oak		2			0.8664	0.07575	4	11.44	0.0003	A
Season*TreeSp	Pine		2			0.01077	0.07573	4	0.14	0.8938	B
Season*TreeSp	Oak		1			-0.4094	0.07588	4	-5.39	0.0057	BC
Season*TreeSp	Pine		1			-0.4756	0.07581	4	-6.27	0.0033	C
Bolt		A				0.05415	0.04637	46	1.17	0.2489	A
Bolt		B				-0.00807	0.04643	46	-0.17	0.8627	A
Bolt		C				-0.05191	0.04647	46	-1.12	0.2698	A
Section					6	0.07471	0.04469	355	1.67	0.0954	A
Section					3	-0.00598	0.04469	355	-0.13	0.8936	AB
Section					5	-0.00646	0.04469	355	-0.14	0.8851	AB
Section					2	-0.01497	0.04469	355	-0.34	0.7378	AB
Section					4	-0.01943	0.04469	355	-0.43	0.664	AB
Section					1	-0.03953	0.04469	355	-0.88	0.377	B
Week				16		0.3688	0.04669	3358	7.9	<.0001	A
Week				20		0.3624	0.04669	3358	7.76	<.0001	A
Week				12		0.3141	0.04655	3358	6.75	<.0001	A
Week				24		0.2825	0.04655	3358	6.07	<.0001	A
Week				8		0.09737	0.04655	3358	2.09	0.0365	B
Week				3		-0.3322	0.04655	3358	-7.14	<.0001	C
Week				4		-0.3638	0.04655	3358	-7.82	<.0001	C
Week				2		-0.3694	0.04655	3358	-7.94	<.0001	C
Week				1		-0.3772	0.04824	3358	-7.82	<.0001	C
Season*Week			1	1		-0.3809	0.07053	3358	-5.4	<.0001	A
Season*Week			1	2		-0.4008	0.06583	3358	-6.09	<.0001	AB
Season*Week			1	3		-0.4218	0.06583	3358	-6.41	<.0001	AB
Season*Week			1	4		-0.4515	0.06583	3358	-6.86	<.0001	B

Table E.3. continued

Season*Week		1	12	-0.4694	0.06583	3358	-7.13	<.0001	C
Season*Week		1	16	-0.4798	0.06583	3358	-7.29	<.0001	D
Season*Week		1	8	-0.5034	0.06583	3358	-7.65	<.0001	D
Season*Week		2	16	1.2174	0.06622	3358	18.38	<.0001	D
Season*Week		2	20	1.168	0.06583	3358	17.74	<.0001	D
Season*Week		2	12	1.0976	0.06583	3358	16.67	<.0001	D
Season*Week		2	24	0.9964	0.06583	3358	15.14	<.0001	D
Season*Week		2	8	0.6981	0.06583	3358	10.61	<.0001	D
Season*Week		2	3	-0.2427	0.06583	3358	-3.69	0.0002	D
Season*Week		2	4	-0.2761	0.06583	3358	-4.2	<.0001	D
Season*Week		2	2	-0.338	0.06583	3358	-5.13	<.0001	D
Season*Week		2	1	-0.3736	0.06583	3358	-5.68	<.0001	D
Season*Week		1	24	-0.4313	0.06583	3358	-6.55	<.0001	D
Season*Week		1	20	-0.4433	0.06622	3358	-6.69	<.0001	D
Week*TreeSp	Oak		12	0.8679	0.06583	3358	13.18	<.0001	A
Week*TreeSp	Oak		16	0.8291	0.06622	3358	12.52	<.0001	A
Week*TreeSp	Oak		20	0.7235	0.06583	3358	10.99	<.0001	A
Week*TreeSp	Oak		8	0.4115	0.06583	3358	6.25	<.0001	B
Week*TreeSp	Oak		24	0.3782	0.06583	3358	5.75	<.0001	B
Week*TreeSp	Pine		24	0.1869	0.06583	3358	2.84	0.0046	BC
Week*TreeSp	Pine		20	0.001184	0.06622	3358	0.02	0.9857	CD
Week*TreeSp	Pine		16	-0.09147	0.06583	3358	-1.39	0.1647	DE
Week*TreeSp	Pine		8	-0.2168	0.06583	3358	-3.29	0.001	EF
Week*TreeSp	Pine		12	-0.2397	0.06583	3358	-3.64	0.0003	EFG
Week*TreeSp	Oak		1	-0.2603	0.06923	3358	-3.76	0.0002	DEFGH
Week*TreeSp	Oak		2	-0.2829	0.06583	3358	-4.3	<.0001	DEFGH
Week*TreeSp	Oak		3	-0.2951	0.06583	3358	-4.48	<.0001	DEFGH
Week*TreeSp	Oak		4	-0.3153	0.06583	3358	-4.79	<.0001	DEFGH
Week*TreeSp	Pine		3	-0.3694	0.06583	3358	-5.61	<.0001	FGH
Week*TreeSp	Pine		4	-0.4124	0.06583	3358	-6.26	<.0001	GH
Week*TreeSp	Pine		2	-0.4558	0.06583	3358	-6.92	<.0001	H
Week*TreeSp	Pine		1	-0.4941	0.06719	3358	-7.35	<.0001	H
Season*Week*TreeSp	Oak	2	12	2.209	0.1025	3358	-2.51	0.012	A
Season*Week*TreeSp	Oak	2	16	2.1491	0.09692	3358	-5.2	<.0001	AB

Table E.3. continued

Season*Week*TreeSp	Oak	2	20	1.8683	0.09309	3358	-3.42	0.0006	B
Season*Week*TreeSp	Oak	2	8	1.3285	0.09309	3358	-5.19	<.0001	C
Season*Week*TreeSp	Oak	2	24	1.1477	0.09309	3358	-4.11	<.0001	C
Season*Week*TreeSp	Pine	2	24	0.845	0.09309	3358	-4.95	<.0001	C
Season*Week*TreeSp	Pine	2	20	0.4677	0.09309	3358	-4.77	<.0001	D
Season*Week*TreeSp	Pine	2	16	0.2857	0.09309	3358	-4.93	<.0001	DE
Season*Week*TreeSp	Pine	2	8	0.0678	0.09309	3358	-5.43	<.0001	EF
Season*Week*TreeSp	Pine	2	12	-0.01383	0.09309	3358	-5.39	<.0001	EFG
Season*Week*TreeSp	Oak	2	4	-0.1867	0.09309	3358	-5.08	<.0001	EFGH
Season*Week*TreeSp	Oak	2	3	-0.2079	0.09309	3358	-5	<.0001	EFGH
Season*Week*TreeSp	Oak	2	2	-0.2477	0.09309	3358	-5.27	<.0001	FGH
Season*Week*TreeSp	Oak	1	1	-0.2577	0.09309	3358	-5.03	<.0001	FGH
Season*Week*TreeSp	Oak	2	1	-0.263	0.09309	3358	-4.53	<.0001	FGH
Season*Week*TreeSp	Pine	2	3	-0.2775	0.09421	3358	-4.94	<.0001	GH
Season*Week*TreeSp	Oak	1	2	-0.3182	0.09309	3358	-4.2	<.0001	FGH
Season*Week*TreeSp	Pine	2	4	-0.3656	0.09309	3358	-5.06	<.0001	H
Season*Week*TreeSp	Oak	1	3	-0.3824	0.09309	3358	-2.83	0.0047	FGH
Season*Week*TreeSp	Oak	1	24	-0.3913	0.09309	3358	-5.2	<.0001	FGH
Season*Week*TreeSp	Oak	1	20	-0.4213	0.09309	3358	-2.66	0.0078	FGH
Season*Week*TreeSp	Pine	2	2	-0.4282	0.09309	3358	-4.6	<.0001	H
Season*Week*TreeSp	Oak	1	4	-0.4439	0.09309	3358	-2.23	0.0256	GH
Season*Week*TreeSp	Pine	1	4	-0.4591	0.09309	3358	-2.98	0.0029	GH
Season*Week*TreeSp	Pine	1	3	-0.4612	0.09309	3358	-2.01	0.045	GH
Season*Week*TreeSp	Pine	1	20	-0.4654	0.09309	3358	-3.93	<.0001	GH
Season*Week*TreeSp	Pine	1	12	-0.4655	0.09309	3358	14.27	<.0001	GH
Season*Week*TreeSp	Pine	1	16	-0.4686	0.09309	3358	0.73	0.4665	GH
Season*Week*TreeSp	Pine	1	24	-0.4713	0.09309	3358	23.73	<.0001	GH
Season*Week*TreeSp	Oak	1	12	-0.4732	0.09309	3358	-0.15	0.8819	GH
Season*Week*TreeSp	Pine	1	2	-0.4834	0.09421	3358	22.81	<.0001	GH
Season*Week*TreeSp	Pine	2	1	-0.4841	0.09309	3358	3.07	0.0022	H
Season*Week*TreeSp	Oak	1	16	-0.491	0.09309	3358	20.07	<.0001	GH
Season*Week*TreeSp	Pine	1	8	-0.5013	0.09309	3358	5.02	<.0001	GH
Season*Week*TreeSp	Pine	1	1	-0.5041	0.09309	3358	12.33	<.0001	GH
Season*Week*TreeSp	Oak	1	8	-0.5055	0.09309	3358	9.08	<.0001	GH

Table E.4. Factor Score 2: Type III Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Season	1	4	27.55	0.0063
TreeSp	1	4	83.73	0.0008
Season*TreeSp	1	4	9.02	0.0398
Bolt	2	46	2.96	0.0618
Section	5	355	1.98	0.0809
Week	8	3358	112.64	<.0001
Season*Week	8	3358	29.42	<.0001
Week*TreeSp	8	3358	133.81	<.0001
Season*Week*TreeSp	8	3358	27.83	<.0001

Table E.5. Factor Score 2: Least squares means

Effect	TreeSp	Bolt	Season	Week	Section	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
Season			2			0.1329	0.03376	4	-3.47	0.0256	A
Season			1			-0.1171	0.03359	4	3.95	0.0168	B
TreeSp	Oak					0.2245	0.03361	4	6.68	0.0026	A
TreeSp	Pine					-0.2087	0.03354	4	-6.22	0.0034	B
Season*TreeSp	Oak		2			0.4206	0.04769	4	0.6	0.5836	A
Season*TreeSp	Oak		1			0.02839	0.04752	4	-5.53	0.0052	B
Season*TreeSp	Pine		2			-0.1548	0.04739	4	8.88	0.0009	BC
Season*TreeSp	Pine		1			-0.2626	0.04735	4	-3.27	0.0308	C
Bolt		C				0.06573	0.03453	46	-1.11	0.2724	A
Bolt		B				-0.00375	0.03465	46	-0.11	0.9144	A
Bolt		A				-0.03837	0.03472	46	1.89	0.0646	A
Section					6	0.08735	0.0371	355	-0.7	0.4835	A
Section					3	0.02712	0.0371	355	-0.65	0.5176	A
Section					5	0.001965	0.0371	355	0.73	0.4653	A
Section					4	-0.01913	0.0371	355	-0.52	0.6065	A
Section					2	-0.02403	0.0371	355	0.05	0.9578	A

Table E.5. continued

Section				1	-0.02602	0.0371	355	2.35	0.0191	A
Week			1		0.9095	0.04308	3358	21.11	<.0001	A
Week			2		0.3696	0.04037	3358	9.16	<.0001	B
Week			3		0.1466	0.04037	3358	3.63	0.0003	C
Week			24		-0.1332	0.04037	3358	-4.18	<.0001	D
Week			20		-0.1434	0.04037	3358	-8.21	<.0001	D
Week			4		-0.1687	0.04037	3358	-8.06	<.0001	D
Week			16		-0.2525	0.0406	3358	-6.22	<.0001	DE
Week			12		-0.3255	0.0406	3358	-3.53	0.0004	E
Week			8		-0.3315	0.04037	3358	-3.3	0.001	E
Season*Week		2	1		1.5046	0.06453	3358	4.87	<.0001	A
Season*Week		2	2		0.6436	0.05709	3358	1.67	0.0942	B
Season*Week		1	1		0.3145	0.05709	3358	2.45	0.0143	C
Season*Week		2	3		0.1532	0.05709	3358	-1.26	0.2087	CD
Season*Week		1	3		0.1399	0.05709	3358	-6.56	<.0001	CDE
Season*Week		1	2		0.09559	0.05709	3358	-5.17	<.0001	CDE
Season*Week		2	20		-0.02698	0.05709	3358	-6.43	<.0001	DEF
Season*Week		2	24		-0.03082	0.05774	3358	-4.5	<.0001	DEF
Season*Week		1	4		-0.07178	0.05709	3358	-4.12	<.0001	DEFG
Season*Week		2	16		-0.1381	0.05709	3358	26.35	<.0001	EFGH
Season*Week		1	24		-0.2355	0.05709	3358	11.27	<.0001	FGH
Season*Week		1	20		-0.2599	0.05709	3358	2.68	0.0073	FGH
Season*Week		2	4		-0.2655	0.05709	3358	-4.65	<.0001	FGH
Season*Week		2	8		-0.2885	0.05709	3358	-5.05	<.0001	GH
Season*Week		1	12		-0.2953	0.05709	3358	-6.23	<.0001	FGH
Season*Week		2	12		-0.3557	0.05774	3358	-2.39	0.0168	H
Season*Week		1	16		-0.3669	0.05709	3358	-0.47	0.6365	H
Season*Week		1	8		-0.3746	0.05709	3358	-0.54	0.5893	H
Week*TreeSp	Oak		1		2.122	0.06245	3358	33.98	<.0001	A
Week*TreeSp	Oak		2		0.9909	0.05925	3358	-5.11	<.0001	B
Week*TreeSp	Oak		3		0.5042	0.05703	3358	17.37	<.0001	C
Week*TreeSp	Pine		24		-0.1251	0.05703	3358	-4.41	<.0001	DE
Week*TreeSp	Pine		20		-0.1277	0.05703	3358	8.84	<.0001	DE
Week*TreeSp	Oak		4		-0.1339	0.05703	3358	-3.7	0.0002	D

Table E.5. continued

Week*TreeSp	Oak		24	-0.1412	0.05703	3358	-2.35	0.0189	D
Week*TreeSp	Oak		20	-0.1591	0.05703	3358	-3.57	0.0004	DE
Week*TreeSp	Pine		16	-0.1695	0.05703	3358	-7.06	<.0001	DEF
Week*TreeSp	Pine		4	-0.2034	0.05703	3358	-4.56	<.0001	DEF
Week*TreeSp	Pine		3	-0.211	0.05703	3358	-7.44	<.0001	DEF
Week*TreeSp	Pine		12	-0.227	0.05703	3358	-3.98	<.0001	DEF
Week*TreeSp	Pine		2	-0.2517	0.05768	3358	-5.82	<.0001	DEF
Week*TreeSp	Pine		8	-0.2601	0.05703	3358	-2.97	0.003	DEF
Week*TreeSp	Pine		1	-0.303	0.05703	3358	-2.79	0.0053	DEF
Week*TreeSp	Oak		16	-0.3356	0.05768	3358	-2.21	0.0269	DEF
Week*TreeSp	Oak		8	-0.4029	0.05703	3358	-2.48	0.0134	EF
Week*TreeSp	Oak		12	-0.424	0.05703	3358	-2.19	0.0283	F
Season*Week*TreeSp	Oak	2	1	3.2338	0.09536	3358	10.59	<.0001	A
Season*Week*TreeSp	Oak	2	2	1.5353	0.08683	3358	-4.39	<.0001	B
Season*Week*TreeSp	Oak	1	1	1.0103	0.08065	3358	5.54	<.0001	C
Season*Week*TreeSp	Oak	2	3	0.5143	0.08065	3358	-3.17	0.0016	D
Season*Week*TreeSp	Oak	1	3	0.494	0.08065	3358	6.12	<.0001	D
Season*Week*TreeSp	Oak	1	2	0.4465	0.08065	3358	-2.65	0.008	DE
Season*Week*TreeSp	Oak	1	4	0.05572	0.08065	3358	0.69	0.4897	F
Season*Week*TreeSp	Oak	2	20	0.02579	0.08065	3358	-2.47	0.0135	EFG
Season*Week*TreeSp	Oak	2	24	-0.00999	0.08065	3358	-4.41	<.0001	FG
Season*Week*TreeSp	Pine	2	24	-0.05165	0.08065	3358	-4.88	<.0001	FGH
Season*Week*TreeSp	Pine	2	16	-0.07518	0.08065	3358	-3.82	0.0001	FGH
Season*Week*TreeSp	Pine	2	20	-0.07976	0.08065	3358	-3.5	0.0005	FGH
Season*Week*TreeSp	Pine	2	8	-0.127	0.08065	3358	-5.83	<.0001	FGHI
Season*Week*TreeSp	Pine	2	12	-0.1718	0.08065	3358	-3.27	0.0011	FGHI
Season*Week*TreeSp	Pine	1	20	-0.1757	0.08065	3358	-4.27	<.0001	FGHI
Season*Week*TreeSp	Pine	1	24	-0.1986	0.08248	3358	-2.13	0.0333	FGHI
Season*Week*TreeSp	Pine	1	4	-0.1993	0.08065	3358	-3.38	0.0007	FGHI
Season*Week*TreeSp	Oak	2	16	-0.201	0.08065	3358	-2.46	0.0138	FGHI
Season*Week*TreeSp	Pine	2	4	-0.2075	0.08065	3358	40.09	<.0001	FGHI
Season*Week*TreeSp	Pine	2	3	-0.208	0.08065	3358	-2.79	0.0054	FGHI
Season*Week*TreeSp	Pine	1	3	-0.2141	0.08065	3358	19.04	<.0001	FGHI
Season*Week*TreeSp	Pine	2	1	-0.2247	0.08065	3358	-3.08	0.0021	FGHI

Table E.5. continued

Season*Week*TreeSp	Pine	2	2	-0.2481	0.08065	3358	6.38	<.0001	FGHI
Season*Week*TreeSp	Pine	1	2	-0.2553	0.08065	3358	-2.58	0.01	FGHI
Season*Week*TreeSp	Pine	1	16	-0.2637	0.08065	3358	-4.01	<.0001	FGHI
Season*Week*TreeSp	Oak	1	24	-0.2723	0.08065	3358	-2.57	0.0101	FGHI
Season*Week*TreeSp	Pine	1	12	-0.2822	0.08065	3358	-5.58	<.0001	FGHI
Season*Week*TreeSp	Oak	1	12	-0.3085	0.08065	3358	-1.57	0.1155	FGHI
Season*Week*TreeSp	Oak	2	4	-0.3235	0.08065	3358	-6.69	<.0001	FGHI
Season*Week*TreeSp	Oak	1	20	-0.3441	0.08065	3358	-2.13	0.0332	GHI
Season*Week*TreeSp	Oak	1	8	-0.3559	0.08248	3358	-2.44	0.0149	GHI
Season*Week*TreeSp	Pine	1	1	-0.3814	0.08065	3358	-0.93	0.3513	FGHI
Season*Week*TreeSp	Pine	1	8	-0.3933	0.08065	3358	0.32	0.7491	GHI
Season*Week*TreeSp	Oak	2	8	-0.4499	0.08065	3358	-0.99	0.3228	HI
Season*Week*TreeSp	Oak	1	16	-0.4702	0.08065	3358	-0.12	0.9014	HI
Season*Week*TreeSp	Oak	2	12	-0.5396	0.08065	3358	-0.64	0.522	I

Table E.6. Factor Score 5: Type III Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Season	1	4	14.35	0.0193
TreeSp	1	4	14.86	0.0182
Season*TreeSp	1	4	11.33	0.0282
Bolt	2	46	0.08	0.9198
Section	5	355	1.68	0.1391
Week	8	3358	52.52	<.0001
Season*Week	8	3358	62.58	<.0001
Week*TreeSp	8	3358	72.35	<.0001
Season*Week*TreeSp	8	3358	72.49	<.0001

Table E.7. Factor Score 5: Least squares means

Effect	TreeSp	Bolt	Season	Week	Section	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
Season			2			0.1873	0.07066	4	-2.7	0.0539	A
Season			1			-0.191	0.07057	4	2.65	0.0568	B
TreeSp	Pine					0.1723	0.06736	4	-2.61	0.0592	A
TreeSp	Oak					-0.176	0.06732	4	2.56	0.0627	B
Season*TreeSp	Pine		2			0.5135	0.09534	4	-2.24	0.0891	A
Season*TreeSp	Oak		2			-0.139	0.09526	4	-1.77	0.151	B
Season*TreeSp	Pine		1			-0.1689	0.09519	4	-1.46	0.2181	B
Season*TreeSp	Oak		1			-0.2131	0.09517	4	5.4	0.0057	B
Bolt		A				0.004671	0.05323	46	0.09	0.9305	A
Bolt		C				-0.0017	0.0533	46	-0.16	0.8739	A
Bolt		B				-0.00851	0.05335	46	-0.03	0.9747	A
Section					6	0.07955	0.05796	355	-0.13	0.8958	A
Section					3	-0.00342	0.05796	355	-0.31	0.7597	A
Section					1	-0.0076	0.05796	355	-0.06	0.9529	A
Section					2	-0.01774	0.05796	355	-0.66	0.5073	A
Section					5	-0.0234	0.05796	355	-0.4	0.6867	A
Section					4	-0.03847	0.05796	355	1.37	0.1707	A
Week				3		0.6045	0.062	3358	-1.01	0.311	A
Week				4		0.1955	0.06008	3358	2.23	0.0258	B
Week				2		0.134	0.06008	3358	10.06	<.0001	B
Week				1		-0.06282	0.06008	3358	3.25	0.0011	C
Week				12		-0.1397	0.06008	3358	-3.33	0.0009	C
Week				24		-0.1578	0.06008	3358	-2.32	0.0202	C
Week				20		-0.1713	0.06024	3358	-3.64	0.0003	C
Week				8		-0.1998	0.06024	3358	-2.84	0.0045	C
Week				16		-0.2192	0.06008	3358	-2.63	0.0087	C
Season*Week			2	3		1.4457	0.09031	3358	-1.34	0.1788	A
Season*Week			2	4		0.6385	0.08497	3358	-2.19	0.0286	B
Season*Week			2	2		0.454	0.08497	3358	-2.79	0.0054	B
Season*Week			2	1		-0.0042	0.08497	3358	-2.91	0.0036	C

Table E.7. continued

Season*Week		2	12	-0.1167	0.08497	3358	-1.68	0.0924	CD
Season*Week		1	1	-0.1214	0.08497	3358	-1.91	0.0557	CD
Season*Week		2	24	-0.1332	0.08497	3358	-3.2	0.0014	CD
Season*Week		1	8	-0.143	0.08542	3358	-1.96	0.0499	CD
Season*Week		1	12	-0.1626	0.08497	3358	-2.15	0.0318	CD
Season*Week		2	16	-0.1669	0.08497	3358	-0.05	0.9606	CD
Season*Week		1	20	-0.1675	0.08497	3358	5.34	<.0001	CD
Season*Week		2	20	-0.175	0.08497	3358	17.01	<.0001	CD
Season*Week		1	24	-0.1825	0.08497	3358	7.51	<.0001	CD
Season*Week		1	2	-0.1861	0.08497	3358	-3.02	0.0025	CD
Season*Week		1	3	-0.2367	0.08497	3358	-1.37	0.1697	CD
Season*Week		1	4	-0.2474	0.08542	3358	-1.95	0.0508	CD
Season*Week		2	8	-0.2566	0.08497	3358	-2.06	0.0395	D
Season*Week		1	16	-0.2716	0.08497	3358	-1.57	0.1171	CD
Week*TreeSp	Pine		3	1.5007	0.08627	3358	-0.24	0.8118	A
Week*TreeSp	Pine		4	0.6421	0.08384	3358	-1.25	0.2101	B
Week*TreeSp	Pine		2	0.3877	0.08227	3358	-1.46	0.1456	C
Week*TreeSp	Oak		1	-0.02054	0.08227	3358	4.71	<.0001	D
Week*TreeSp	Pine		1	-0.1051	0.08227	3358	-3.55	0.0004	DE
Week*TreeSp	Pine		12	-0.1072	0.08227	3358	18.24	<.0001	DE
Week*TreeSp	Oak		2	-0.1197	0.08227	3358	-3.05	0.0023	DE
Week*TreeSp	Oak		24	-0.1439	0.08227	3358	7.81	<.0001	DE
Week*TreeSp	Pine		20	-0.1697	0.08227	3358	-2.09	0.0371	DE
Week*TreeSp	Oak		8	-0.1716	0.08227	3358	-2.77	0.0056	DE
Week*TreeSp	Pine		24	-0.1717	0.08227	3358	-2.09	0.0366	DE
Week*TreeSp	Oak		12	-0.1721	0.08227	3358	-1.3	0.1925	DE
Week*TreeSp	Oak		20	-0.1728	0.08273	3358	-2.91	0.0036	DE
Week*TreeSp	Pine		16	-0.1976	0.08227	3358	-2.4	0.0163	DE
Week*TreeSp	Pine		8	-0.2281	0.08227	3358	-2.1	0.0357	DE
Week*TreeSp	Oak		16	-0.2408	0.08273	3358	-2.05	0.0403	DE
Week*TreeSp	Oak		4	-0.251	0.08227	3358	-1.75	0.0804	DE
Week*TreeSp	Oak		3	-0.2918	0.08227	3358	-2.09	0.0369	E
Season*Week*TreeSp	Pine	2	3	3.1934	0.1274	3358	-0.44	0.661	A
Season*Week*TreeSp	Pine	2	4	1.536	0.1208	3358	-1.55	0.1216	B

Table E.7. continued

Season*Week*TreeSp	Pine	2	2	0.9735	0.1163	3358	-1.5	0.1347	C
Season*Week*TreeSp	Oak	2	1	0.01481	0.1163	3358	-1.7	0.0888	D
Season*Week*TreeSp	Pine	2	1	-0.02321	0.1163	3358	-2.42	0.0156	D
Season*Week*TreeSp	Oak	1	1	-0.05589	0.1163	3358	-1.65	0.0992	D
Season*Week*TreeSp	Oak	2	2	-0.0654	0.1163	3358	-2.09	0.0368	D
Season*Week*TreeSp	Pine	1	8	-0.07997	0.1163	3358	-2.16	0.0305	D
Season*Week*TreeSp	Pine	1	12	-0.09473	0.1163	3358	-1.77	0.0766	D
Season*Week*TreeSp	Oak	2	16	-0.1124	0.1163	3358	-0.69	0.4919	D
Season*Week*TreeSp	Oak	2	24	-0.1127	0.1163	3358	-1.98	0.0477	D
Season*Week*TreeSp	Oak	2	12	-0.1137	0.1163	3358	-0.81	0.4156	D
Season*Week*TreeSp	Pine	2	12	-0.1198	0.1163	3358	-3.17	0.0015	D
Season*Week*TreeSp	Oak	2	8	-0.137	0.1163	3358	-1.49	0.1353	D
Season*Week*TreeSp	Pine	1	20	-0.1527	0.1163	3358	-1.57	0.1171	D
Season*Week*TreeSp	Pine	2	24	-0.1537	0.1177	3358	-1.3	0.1944	D
Season*Week*TreeSp	Oak	2	20	-0.1633	0.1163	3358	-1.51	0.1324	D
Season*Week*TreeSp	Pine	1	16	-0.1738	0.1163	3358	-1.63	0.1029	D
Season*Week*TreeSp	Oak	1	2	-0.1741	0.1163	3358	0.13	0.8987	D
Season*Week*TreeSp	Oak	1	24	-0.1751	0.1163	3358	-0.2	0.8419	D
Season*Week*TreeSp	Oak	1	20	-0.1823	0.1163	3358	-0.56	0.5741	D
Season*Week*TreeSp	Pine	2	20	-0.1868	0.1163	3358	8.37	<.0001	D
Season*Week*TreeSp	Pine	1	1	-0.187	0.1163	3358	-2.6	0.0095	D
Season*Week*TreeSp	Pine	1	24	-0.1898	0.1163	3358	27.45	<.0001	D
Season*Week*TreeSp	Pine	1	3	-0.1919	0.1163	3358	-2.23	0.0261	D
Season*Week*TreeSp	Pine	1	2	-0.1981	0.1163	3358	13.2	<.0001	D
Season*Week*TreeSp	Oak	1	8	-0.2061	0.1163	3358	-1.18	0.2391	D
Season*Week*TreeSp	Pine	2	16	-0.2215	0.1163	3358	-3.23	0.0012	D
Season*Week*TreeSp	Oak	1	12	-0.2305	0.1163	3358	-0.98	0.3287	D
Season*Week*TreeSp	Oak	1	4	-0.2431	0.1163	3358	-1.03	0.3034	D
Season*Week*TreeSp	Pine	1	4	-0.2517	0.1177	3358	-0.95	0.3397	D
Season*Week*TreeSp	Oak	2	4	-0.259	0.1163	3358	-1.9	0.0571	D
Season*Week*TreeSp	Oak	1	3	-0.2815	0.1163	3358	-1.4	0.1605	D
Season*Week*TreeSp	Oak	2	3	-0.3021	0.1163	3358	-1.61	0.1085	D
Season*Week*TreeSp	Oak	1	16	-0.3693	0.1163	3358	-0.97	0.3328	D
Season*Week*TreeSp	Pine	2	8	-0.3762	0.1163	3358	-1.32	0.1867	D

Table E.8. Factor Score 6: Type III Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Season	1	4	10.53	0.0315
TreeSp	1	4	22.63	0.0089
Season*TreeSp	1	4	14.66	0.0186
Bolt	2	46	0.29	0.7497
			Table E.8. continued	
Section	5	355	16.1	<.0001
Week	8	3358	101.79	<.0001
Season*Week	8	3358	96.57	<.0001
Week*TreeSp	8	3358	125.73	<.0001
Season*Week*TreeSp	8	3358	115.6	<.0001

Table E.9. Factor Score 6: Least squares means

Effect	TreeSp	Bolt	Season	Week	Section	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
Season			2			0.1637	0.07313	4	-2.35	0.0786	A
Season			1			-0.1718	0.07307	4	2.24	0.0886	B
TreeSp	Pine					0.2418	0.07311	4	-3.42	0.0268	A
TreeSp	Oak					-0.2499	0.07308	4	3.31	0.0297	B
Season*TreeSp	Pine		2			0.6075	0.1034	4	-2.12	0.1009	A
Season*TreeSp	Pine		1			-0.1238	0.1034	4	-1.2	0.2972	B
Season*TreeSp	Oak		1			-0.2197	0.1033	4	-2.71	0.0535	B
Season*TreeSp	Oak		2			-0.2801	0.1033	4	5.88	0.0042	B
Bolt		C				0.00991	0.05494	46	-0.15	0.882	A
Bolt		A				-0.0082	0.055	46	-0.25	0.8024	A
Bolt		B				-0.01384	0.05504	46	0.18	0.8579	A
Section					6	0.1887	0.05824	355	-2.06	0.0397	A
Section					5	0.06909	0.05824	355	-1.69	0.0927	B

Table E.9. continued

Section				4	0.00836	0.05824	355	-1.24	0.2176	BC
Section				3	-0.07194	0.05824	355	0.14	0.8859	CD
Section				2	-0.09818	0.05824	355	1.19	0.2363	CD
Section				1	-0.1203	0.05824	355	3.24	0.0013	D
Week			8		0.7594	0.06053	3358	-3.22	0.0013	A
Week			4		0.244	0.05908	3358	-3.02	0.0026	B
Week			12		0.04036	0.05908	3358	-2.21	0.027	C
Week			16		-0.1147	0.05908	3358	4.13	<.0001	D
Week			3		-0.1307	0.05908	3358	12.85	<.0001	D
Week			20		-0.1775	0.05908	3358	0.68	0.4945	DE
Week			2		-0.1782	0.0592	3358	-1.94	0.0527	DE
Week			1		-0.1947	0.0592	3358	-3	0.0027	DE
Week			24		-0.2842	0.05908	3358	-4.81	<.0001	E
Season*Week		2	8		1.6834	0.08761	3358	-2.48	0.0131	A
Season*Week		2	4		0.5407	0.08355	3358	-2.16	0.0307	B
Season*Week		2	12		0.2706	0.08355	3358	-0.62	0.5341	C
Season*Week		2	16		0.032	0.08355	3358	-0.63	0.5278	D
Season*Week		1	3		-0.05195	0.08355	3358	-1.97	0.049	CDEF
Season*Week		1	4		-0.05276	0.08355	3358	-2.27	0.0231	CDEF
Season*Week		2	20		-0.136	0.08355	3358	-3.13	0.0018	DE
Season*Week		1	8		-0.1646	0.08388	3358	-2.61	0.0091	DEF
Season*Week		2	1		-0.172	0.08355	3358	-2.49	0.0128	DEF
Season*Week		2	2		-0.1758	0.08355	3358	-2.06	0.0396	DEF
Season*Week		1	2		-0.1807	0.08355	3358	-2.1	0.0354	DEF
Season*Week		1	12		-0.1899	0.08355	3358	-2.51	0.0122	DEF
Season*Week		1	24		-0.208	0.08355	3358	6.47	<.0001	DEF
Season*Week		2	3		-0.2094	0.08355	3358	20.15	<.0001	EF
Season*Week		1	1		-0.2175	0.08355	3358	3.24	0.0012	DEF
Season*Week		1	20		-0.2191	0.08388	3358	0.38	0.7029	DEF
Season*Week		1	16		-0.2615	0.08355	3358	-1.63	0.1037	DEF
Season*Week		2	24		-0.3604	0.08355	3358	-4.31	<.0001	F
Week*TreeSp	Pine		8		1.8496	0.08649	3358	-2.01	0.0441	A
Week*TreeSp	Pine		4		0.769	0.08471	3358	-2.54	0.0111	B
Week*TreeSp	Pine		12		0.3514	0.08355	3358	-2	0.0458	C

Table E.9. continued

Week*TreeSp	Pine		16	0.07396	0.08355	3358	-2.27	0.0233	D
Week*TreeSp	Pine		3	-0.04003	0.08355	3358	-2.65	0.0081	DE
Week*TreeSp	Oak		2	-0.1669	0.08355	3358	-0.48	0.6319	DE
Week*TreeSp	Oak		1	-0.1742	0.08355	3358	-3.36	0.0008	DE
Week*TreeSp	Oak		20	-0.1772	0.08355	3358	9.2	<.0001	DE
Week*TreeSp	Pine		20	-0.1779	0.08355	3358	-3.96	<.0001	E
Week*TreeSp	Pine		2	-0.1896	0.08355	3358	22.14	<.0001	E
Week*TreeSp	Pine		1	-0.2153	0.08355	3358	-3.24	0.0012	E
Week*TreeSp	Oak		3	-0.2214	0.08355	3358	4.21	<.0001	DE
Week*TreeSp	Pine		24	-0.2446	0.08388	3358	-3.62	0.0003	E
Week*TreeSp	Oak		12	-0.2707	0.08355	3358	0.89	0.3761	DE
Week*TreeSp	Oak		4	-0.2811	0.08355	3358	-2.12	0.0341	DE
Week*TreeSp	Oak		16	-0.3034	0.08388	3358	-2.12	0.034	DE
Week*TreeSp	Oak		24	-0.3238	0.08355	3358	-3.88	0.0001	DE
Week*TreeSp	Oak		8	-0.3307	0.08355	3358	-2.93	0.0034	DE
Season*Week*TreeSp	Pine	2	8	3.811	0.1263	3358	-1.7	0.0887	A
Season*Week*TreeSp	Pine	2	4	1.4209	0.1214	3358	-1.81	0.0703	B
Season*Week*TreeSp	Pine	2	12	0.8579	0.1182	3358	-1.66	0.0973	C
Season*Week*TreeSp	Pine	2	16	0.3574	0.1182	3358	-1.4	0.1619	D
Season*Week*TreeSp	Pine	1	4	0.1172	0.1182	3358	-1.24	0.2166	DEF
Season*Week*TreeSp	Pine	1	3	0.04211	0.1182	3358	0.36	0.7215	DEF
Season*Week*TreeSp	Pine	1	8	-0.1119	0.1182	3358	-1.88	0.0596	DEF
Season*Week*TreeSp	Oak	2	20	-0.1138	0.1182	3358	0.99	0.3214	DE
Season*Week*TreeSp	Pine	2	3	-0.1222	0.1182	3358	-1.84	0.066	EF
Season*Week*TreeSp	Oak	2	1	-0.1333	0.1182	3358	-0.95	0.3438	DEF
Season*Week*TreeSp	Oak	2	2	-0.1379	0.1182	3358	-1.9	0.0572	DEF
Season*Week*TreeSp	Oak	1	3	-0.146	0.1182	3358	-1.31	0.1896	DEF
Season*Week*TreeSp	Pine	1	12	-0.155	0.1182	3358	-2.65	0.008	DEF
Season*Week*TreeSp	Pine	2	20	-0.1581	0.1182	3358	-1.77	0.0764	EF
Season*Week*TreeSp	Pine	1	2	-0.1653	0.1182	3358	-2.04	0.0419	DEF
Season*Week*TreeSp	Oak	1	2	-0.196	0.1191	3358	-1.66	0.0971	DEF
Season*Week*TreeSp	Pine	1	20	-0.1976	0.1182	3358	-1.71	0.0879	DEF
Season*Week*TreeSp	Oak	1	24	-0.2017	0.1182	3358	-1.81	0.0698	DEF
Season*Week*TreeSp	Pine	1	16	-0.2094	0.1182	3358	-1.13	0.2594	DEF

Table E.9. continued

Season*Week*TreeSp	Pine	2	1	-0.2107	0.1182	3358	-1.78	0.0746	EF
Season*Week*TreeSp	Pine	2	2	-0.2138	0.1182	3358	-1.17	0.2433	EF
Season*Week*TreeSp	Pine	1	24	-0.2144	0.1182	3358	-1.81	0.0705	DEF
Season*Week*TreeSp	Oak	1	1	-0.2151	0.1182	3358	-2.51	0.0121	DEF
Season*Week*TreeSp	Oak	1	8	-0.2173	0.1182	3358	-1.03	0.3012	DEF
Season*Week*TreeSp	Pine	1	1	-0.2198	0.1182	3358	-2.87	0.0041	DEF
Season*Week*TreeSp	Oak	1	4	-0.2227	0.1182	3358	12.03	<.0001	DEF
Season*Week*TreeSp	Oak	1	12	-0.2248	0.1182	3358	-3.76	0.0002	DEF
Season*Week*TreeSp	Oak	1	20	-0.2405	0.1182	3358	32.25	<.0001	DEF
Season*Week*TreeSp	Pine	2	24	-0.2749	0.1182	3358	-2.68	0.0074	EF
Season*Week*TreeSp	Oak	2	16	-0.2934	0.1182	3358	7.26	<.0001	EF
Season*Week*TreeSp	Oak	2	3	-0.2967	0.1191	3358	-2.46	0.0138	EF
Season*Week*TreeSp	Oak	1	16	-0.3135	0.1182	3358	3.02	0.0025	EF
Season*Week*TreeSp	Oak	2	12	-0.3166	0.1182	3358	-0.96	0.3354	EF
Season*Week*TreeSp	Oak	2	4	-0.3395	0.1182	3358	-1.34	0.1808	EF
Season*Week*TreeSp	Oak	2	8	-0.4442	0.1182	3358	-3.77	0.0002	EF
Season*Week*TreeSp	Oak	2	24	-0.4459	0.1182	3358	-2.33	0.02	F

Table E.10. Factor Score 7: Type III Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Season	1	4	0.88	0.4011
TreeSp	1	4	114.96	0.0004
Season*TreeSp	1	4	31.52	0.0049
Bolt	2	46	0.2	0.8159
Section	5	355	28.19	<.0001
Week	8	3358	73.08	<.0001
Season*Week	8	3358	119.56	<.0001
Week*TreeSp	8	3358	41.61	<.0001
Season*Week*TreeSp	8	3358	49.86	<.0001

Table E.11. Factor Score 7: Least squares means

Effect	TreeSp	Bolt	Season	Week	Section	Estimate	Standard Error	DF	t Value	Pr > |t|	Tukey-Kramer
Season			1			0.046	0.07136	4	0.64	0.5543	A
Season			2			-0.04866	0.07129	4	-0.68	0.5323	A
TreeSp	Oak					0.2488	0.05559	4	4.48	0.011	A
TreeSp	Pine					-0.2515	0.05555	4	-4.53	0.0106	B
Season*TreeSp	Oak		2			0.3325	0.0787	4	2.1	0.1038	A
Season*TreeSp	Oak		1			0.1652	0.07861	4	-0.93	0.4047	A
Season*TreeSp	Pine		1			-0.07316	0.07853	4	4.23	0.0133	AB
Season*TreeSp	Pine		2			-0.4298	0.07851	4	-5.47	0.0054	B
Bolt		C				0.01603	0.05775	46	-0.1	0.9231	A
Bolt		A				-0.00561	0.05782	46	-0.25	0.8042	A
Bolt		B				-0.01442	0.05787	46	0.28	0.783	A
Section					6	0.2828	0.05881	355	-3.14	0.0018	A
Section					5	0.1401	0.05881	355	-1.74	0.0832	B
Section					4	-0.06232	0.05881	355	-1.39	0.1662	C
Section					3	-0.08159	0.05881	355	-1.06	0.29	C
Section					2	-0.1022	0.05881	355	2.38	0.0177	C
Section					1	-0.1848	0.05881	355	4.81	<.0001	C
Week				12		0.4801	0.06152	3358	1.9	0.0579	A
Week				8		0.3972	0.0597	3358	-0.7	0.4862	A
Week				1		0.1167	0.0597	3358	-1.13	0.2604	B
Week				16		-0.0243	0.0597	3358	-0.95	0.3446	BC
Week				2		-0.04158	0.0597	3358	6.65	<.0001	C
Week				4		-0.05643	0.0597	3358	8.04	<.0001	C
Week				3		-0.0672	0.05985	3358	-0.41	0.6848	C
Week				20		-0.2744	0.05985	3358	-4.58	<.0001	D
Week				24		-0.542	0.0597	3358	-9.08	<.0001	E
Season*Week			2	12		0.9306	0.08948	3358	-1.11	0.267	A
Season*Week			2	8		0.7123	0.08443	3358	-0.88	0.3788	A
Season*Week			2	1		0.3327	0.08443	3358	-0.68	0.4983	BCD
Season*Week			1	24		0.2921	0.08443	3358	-1.14	0.2562	BE

Table E.11. continued

Season*Week		1	20	0.2632	0.08443	3358	0.97	0.3307	BCE
Season*Week		1	8	0.08213	0.08443	3358	0.35	0.7262	BCDEF
Season*Week		1	16	0.07368	0.08443	3358	0.87	0.3829	BCDEF
Season*Week		1	12	0.02957	0.08485	3358	3.1	0.0019	CDFG
Season*Week		2	2	-0.00883	0.08443	3358	3.46	0.0005	EFG
Season*Week		2	4	-0.01697	0.08443	3358	3.94	<.0001	EFG
Season*Week		1	3	-0.05718	0.08443	3358	-0.1	0.9167	DFG
Season*Week		1	2	-0.07432	0.08443	3358	-0.91	0.3605	DFG
Season*Week		2	3	-0.07722	0.08443	3358	-0.2	0.8407	EFG
Season*Week		1	4	-0.09589	0.08443	3358	8.44	<.0001	F
Season*Week		1	1	-0.09934	0.08443	3358	11.02	<.0001	F
Season*Week		2	16	-0.1223	0.08485	3358	-1.44	0.1497	EFG
Season*Week		2	20	-0.812	0.08443	3358	-9.62	<.0001	H
Season*Week		2	24	-1.3762	0.08443	3358	-16.3	<.0001	I
Week*TreeSp	Oak		12	1.1582	0.07588	3358	2.68	0.0075	A
Week*TreeSp	Oak		8	0.8414	0.07335	3358	0.41	0.6791	B
Week*TreeSp	Oak		16	0.344	0.07162	3358	-2.23	0.0256	C
Week*TreeSp	Oak		1	0.203	0.07162	3358	1.07	0.2838	CD
Week*TreeSp	Pine		2	0.07678	0.07162	3358	-0.26	0.7986	CDE
Week*TreeSp	Oak		20	0.06103	0.07162	3358	-1.62	0.105	DEF
Week*TreeSp	Oak		4	0.0345	0.07162	3358	0.48	0.63	DEF
Week*TreeSp	Pine		1	0.03034	0.07162	3358	-2.06	0.0397	DEFG
Week*TreeSp	Oak		3	-0.01828	0.07162	3358	11.75	<.0001	DEFG
Week*TreeSp	Pine		8	-0.04706	0.07162	3358	-0.66	0.5112	DEFG
Week*TreeSp	Pine		3	-0.1161	0.07162	3358	16.17	<.0001	EFG
Week*TreeSp	Pine		4	-0.1474	0.07162	3358	-2.76	0.0057	EFG
Week*TreeSp	Oak		2	-0.1599	0.07211	3358	4.77	<.0001	EFGH
Week*TreeSp	Pine		12	-0.198	0.07162	3358	-5.48	<.0001	FGH
Week*TreeSp	Oak		24	-0.2247	0.07162	3358	0.85	0.3943	GH
Week*TreeSp	Pine		16	-0.3926	0.07211	3358	-8.46	<.0001	HI
Week*TreeSp	Pine		20	-0.6098	0.07162	3358	-3.14	0.0017	I
Week*TreeSp	Pine		24	-0.8594	0.07162	3358	-12	<.0001	J
Season*Week*TreeSp	Oak	2	12	2.2494	0.113	3358	-1.45	0.146	A
Season*Week*TreeSp	Oak	2	8	1.6018	0.1061	3358	-0.32	0.746	B

Table E.11. continued

Season*Week*TreeSp	Oak	1	24	0.6909	0.1013	3358	-0.87	0.3825	C
Season*Week*TreeSp	Oak	1	20	0.6329	0.1013	3358	-0.59	0.5525	CD
Season*Week*TreeSp	Oak	2	1	0.5704	0.1013	3358	0.33	0.7378	CE
Season*Week*TreeSp	Oak	2	16	0.4339	0.1013	3358	-1.46	0.1433	CDEF
Season*Week*TreeSp	Oak	1	16	0.2541	0.1013	3358	-0.2	0.8398	EFGH
Season*Week*TreeSp	Pine	2	2	0.2137	0.1013	3358	-1.69	0.0909	CDEFG
Season*Week*TreeSp	Pine	2	1	0.09506	0.1013	3358	0.8	0.4236	DFGH
Season*Week*TreeSp	Oak	2	4	0.08948	0.1013	3358	0.82	0.4115	DFGH
Season*Week*TreeSp	Pine	1	8	0.0832	0.1013	3358	0.66	0.5089	EFGHI
Season*Week*TreeSp	Oak	1	8	0.08107	0.1013	3358	-0.08	0.9388	EFGHI
Season*Week*TreeSp	Oak	1	12	0.06691	0.1013	3358	2.51	0.0122	EFGHI
Season*Week*TreeSp	Oak	1	3	0.03391	0.1013	3358	-1.05	0.2923	EFGHIJ
Season*Week*TreeSp	Pine	1	12	-0.00777	0.1013	3358	6.25	<.0001	FGHIJ
Season*Week*TreeSp	Oak	1	4	-0.02048	0.1027	3358	-1.04	0.3001	FGHIJ
Season*Week*TreeSp	Pine	1	1	-0.03437	0.1013	3358	6.82	<.0001	FGHIJ
Season*Week*TreeSp	Pine	1	2	-0.06017	0.1013	3358	-1.05	0.2927	FGHIJ
Season*Week*TreeSp	Oak	2	3	-0.07047	0.1013	3358	5.63	<.0001	GHI
Season*Week*TreeSp	Pine	2	3	-0.08398	0.1013	3358	0.94	0.3481	GHIJ
Season*Week*TreeSp	Oak	1	2	-0.08847	0.1013	3358	-2.28	0.0224	FGHIJ
Season*Week*TreeSp	Pine	1	20	-0.1064	0.1013	3358	2.11	0.0349	FGHIJ
Season*Week*TreeSp	Pine	1	24	-0.1066	0.1013	3358	-0.7	0.4867	FGHIJ
Season*Week*TreeSp	Pine	1	16	-0.1067	0.1013	3358	-0.83	0.4071	FGHIJ
Season*Week*TreeSp	Pine	2	4	-0.1234	0.1013	3358	0.88	0.3771	GHIJ
Season*Week*TreeSp	Pine	1	3	-0.1483	0.1013	3358	-1.22	0.2231	GHIJK
Season*Week*TreeSp	Oak	1	1	-0.1643	0.1013	3358	15.81	<.0001	GHIJK
Season*Week*TreeSp	Pine	1	4	-0.1713	0.1013	3358	-1.75	0.0801	GHIJK
Season*Week*TreeSp	Pine	2	8	-0.1773	0.1013	3358	22.21	<.0001	HIJ
Season*Week*TreeSp	Oak	2	2	-0.2314	0.1013	3358	-3.83	0.0001	HIJ
Season*Week*TreeSp	Pine	2	12	-0.3883	0.1027	3358	4.23	<.0001	IJK
Season*Week*TreeSp	Oak	2	20	-0.5108	0.1013	3358	-6.7	<.0001	JK
Season*Week*TreeSp	Pine	2	16	-0.6784	0.1013	3358	-5.04	<.0001	K
Season*Week*TreeSp	Pine	2	20	-1.1132	0.1013	3358	-10.99	<.0001	L
Season*Week*TreeSp	Oak	2	24	-1.1402	0.1013	3358	-11.26	<.0001	L
Season*Week*TreeSp	Pine	2	24	-1.6122	0.1013	3358	-15.92	<.0001	M

APPENDIX F: COLEOPTERAN ASSEMBLAGES

Table F.1. Results from principal component and regression analyses combine to estimate beetle assemblages. Significant factor loadings for eight extracted factors correlated with log (x+1) transformed frequency data of the 30 most abundant beetle taxa produce information that pertain to beetle succession on freshly killed Loblolly Pine and Southern Red.

Family	Taxa	Factor Loading	Description of Significant Effects
		Factor 1	
Zopheridae	*Pycnomerus reflexus*	0.72935	Most significant factor for SEASON (P=0.0003). All associated beetle taxa were more abundant during Season 2 collected from Oak. Taxa were more abundant on section 6 and were prevalent during weeks 16, 20, 12, 24 (in descending significance). Significance was also noted in taxa collected from week 16 of season 2, weeks 12, 16, 20 of season 2 from oak; and from oak in general during week 12.
Histeridae	*Bacanius punctiformis*	0.67323	
Cerylonidae	*Cerylon unicolor*	0.64665	
Carabidae	*Mioptachys flavicauda*	0.61243	
Ptiliidae	Ptiliidae spp.	0.60733	
Curculionidae	*Cossonus impressifrons*	0.55645	
Staphylinidae	*Thoracophorus costalis*	0.33737	
		Factor 2	
Nitidulidae	*Colopterus semitectus* *	0.73451	Second most significant factor for SEASON (P=0.0063) and TREESP (P=0.0008). Taxa were more abundant in season 2. Three taxa were collected exclusively from Oak, and the other two were collected over 94 % from Oak. The four taxa with the most significant factor loadings were all Nitidulidae. Taxa were most prevalent during week 1, especially colonizing Oak trees during season 2.
Nitidulidae	*Carpophilus tempestivus* *	0.72341	
Nitidulidae	*Colopterus truncatus*	0.65428	
Nitidulidae	*Colopterus niger* *	0.56939	
Staphylinidae	*Placusa* sp.	0.49399	

Table F.1. continued

		Factor 3		
Laemophloeidae	*Phloeolaemus chamaeropis*	0.6504	99.9% Oak	Although the MIXED procedure was unable to complete analysis of this factor, it was noted that an average of 75% of specimens from the associated taxa were collected from Oak in this factor. Six of eight taxa were more numerous in Season 2. Many specimens were collected during Week 1, 2, 3, and 4.
Staphylinidae	*Myrmecocephalus concinnus*	0.60777	72% Oak	
Silvanidae	*Silvanus muticus*	0.54313	55% Oak	
Curculionidae	*Xyleborus affinis*	0.49255	95% Oak	
Histeridae	*Aeletes floridae*	0.47848	90% Oak	
Staphylinidae	*Laetulonthus laetulus*	0.44994	87% Oak	
Staphylinidae	*Placusa* sp.	0.41627	94.3% Oak	
Nitidulidae	*Carpophilus tempestivus* *	0.38104	100% Oak	
		Factor 4		
Nitidulidae	*Epuraea erichsoni*	0.77321	The MIXED procedure was also unable to complete analysis of this factor, yet it was noted that all taxa were significantly more abundant on Oak during season 1. Many specimens from the three taxa demonstrating the most significant factor loadings occurred during from Week 1-4. The five associated taxa are from two beetle families.	
Nitidulidae	*Carpophilus corticinus*	0.63947		
Staphylinidae	*Placusa* sp.	0.45005		
Nitidulidae	*Colopterus niger* *	0.39989		
Staphylinidae	*Myrmecocephalus concinnus*	0.37114		
		Factor 5		
Tenebrionidae	*Corticeus glaber* **	0.7632	Associated taxa were significantly more abundant during week 3 of season 2 from Pine. The two taxa with the most significant factor loadings were collected exclusively from Pine.	
Histeridae	*Platysoma parallela* **	0.73775		
Curculionidae	*Xyleborinus saxeseni*	0.60246		
Staphylinidae	*Leptusa* spp.	0.32076		
		Factor 6		
Curculionidae	*Cossonus corticola*	0.84841	Both species were significantly more numerous from Pine (over 95 % of specimens), Section 6, during Season 2. Taxa were strongly associated with Pine during Week 8 and with Pine during Season 2.	
Histeridae	*Plegaderus transversus*	0.83825		

Table F.1. continued

		Factor 7		
Histeridae	*Aeletes floridae*	0.5497	Oak; Section 6; Season 2	This factor is the most significant for TREESP (P=.0004), SEASON*TREESP (P=.0049), and SECTION (P=<0.0001). Taxa corresponding to positive loadings were significantly more numerous on Oak, Section 6, in Season 2. Taxa corresponding to negative loadings were similar in being found in Season 2, but *contrasted* by being slightly more abundant on Pine bolts. Overall, taxa were significantly linked to section six, weeks 12 and 8, season 2 week 12 and season 2 week 8, as well as the combination of season 2 week 12 and Oak.
Curculionidae	*Cossonus impressifrons*	0.50412		
Histeridae	*Platysoma lecontei*	0.4504		
Silvanidae	*Silvanus muticus*	0.31746		
Zopheridae	*Pycnomerus haematodes*	**-0.49243**	Pine; Season 2	
Carabidae	*Mioptachys flavicauda*	**-0.33835**		
		Factor 8		
Staphylinidae	*Leptusa* spp.	0.60213	56% Pine	The MIXED procedure was also unable to complete analysis of this factor. All three taxa were more abundant in season 2. Main separation for this factor seems to be a tricky interaction of season and week collected: Season 1, later weeks (16, 20) and Season 2, early weeks (3, 4, 8).
Zopheridae	*Bitoma quadricollis*	0.58867	57% Pine	
Histeridae	*Platysoma coarctatum*	0.4612	99.9% Oak	

* collected exclusively from Oak

** collected exclusively from Pine

APPENDIX G: HABITUS OF SELECTED BEETLE TAXA

The number of specimens collected during both seasons follows the form: abundance on Loblolly Pine, Southern Red Oak / total.

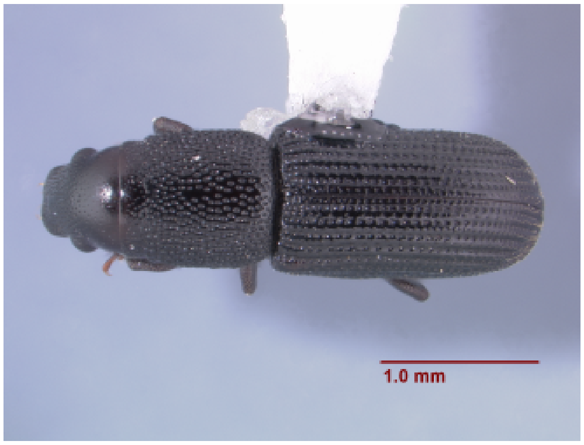


Figure G.1 Curculionidae: *Rhyncolus discors* Casey 45, 3 / 48

Figure G.2 Staphylinidae: *Placusa* sp. 1165, 19260 / 20425

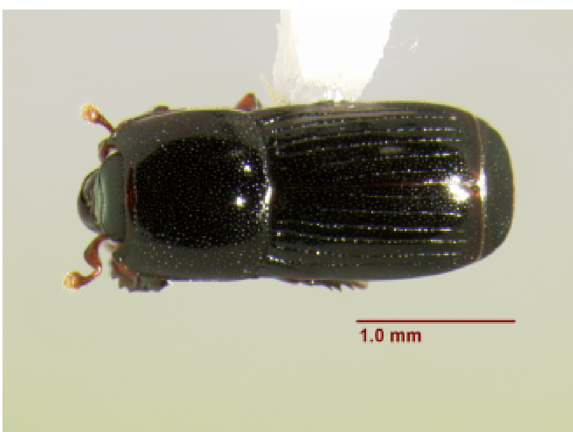


Figure G.3 Histeridae: *Platysoma coarctatum* LeConte 47, 37 / 84

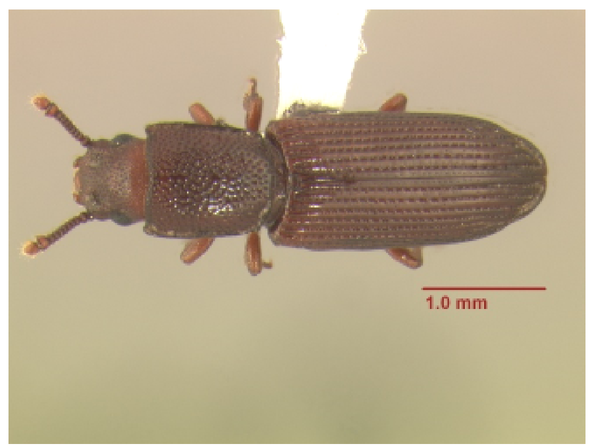


Figure G.4 Zopheridae: *Pycnomerus reflexus* Say 136, 1549 / 1685

Figure G.5 Nitidulidae: *Colopterus niger* (Say) 0, 867 / 867

Figure G.6 *Mochtherus tetraspilotus* (MacLeay) 1, 0 / 1

Figure G.7 *Arthrolips fasciata* (Erichson) 1, 0 / 1

Figure G.8 *Pediacus subglaber* LeConte 5, 11 / 16

Figure G.9 *Drapetes quadripustulatus* Bonvouloir 2, 1 / 3

Figure G.10 *Clemmus minor* Crotch 1, 1 /2

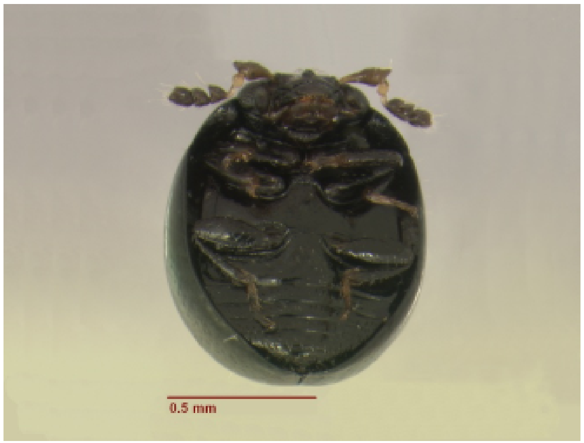


Figure G.11 *Micropsephodes lundgreni* Leschen and Carlton 4, 24 / 28

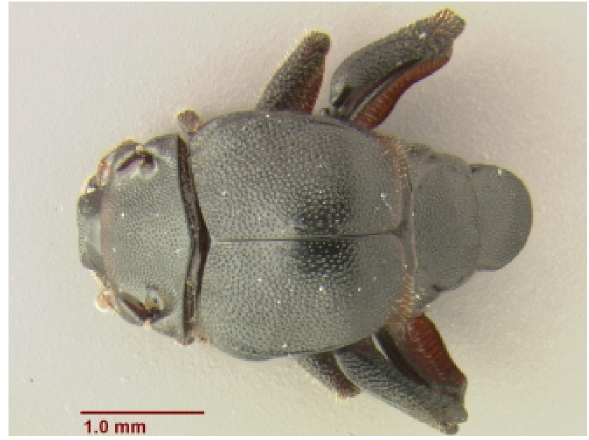


Figure G.12 . *Terapus* n. sp. 0, 2 / 2

VITA

Stephanie Gil was born in New Orleans, Louisiana and is the youngest of six children. She attended Mt. Carmel Academy and the University of New Orleans. Her entry into the world of insects began with the course "Introduction to Entomology," taught by Dr. Jerry Howard. She then worked in his lab curating the students' insect collections. Stephanie graduated from UNO in May 2002 with a Bachelor of Science degree in biological sciences, concentration in premedical biology, and a Bachelor of Arts degree in psychology. Through Dr. Howard's efforts, she began a summer internship at the Louisiana State Arthropod Museum in 2002. In September 2002 she worked with the Medical Entomology lab under the direction of Dr. Michael Perich identifying and counting over 55,000 mosquitoes in the West Nile outbreak project, Operation Mosquito. In fall 2003 Stephanie began working on her master's degree under major professor Dr. Chris Carlton. Throughout her time at LSU she has had the opportunity to learn new techniques for capturing and studying arthropods, travel to research locations, such as the Great Smoky Mountains National Forest, attend various workshops as well as the 2005 National ESA Meeting, join the Entomological Society of America and Gamma Sigma Delta (College of Agriculture Honor Society), and serve as Secretary and member of the Entomology Club. Stephanie is currently completing the requirements for the master's degree in the Department of Entomology.