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Effects of Forest Age and Composition on Coleoptera Associated with Fungal Fruiting Bodies in Southwest Ohio

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EFFECTS OF FOREST AGE AND COMPOSITION ON COLEOPTERA ASSOCIATED WITH FUNGAL FRUITING BODIES IN SOUTHWEST OHIO

A Thesis submitted in partial fulfillment of the
requirements for the degree of
Master of Science

by

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2020

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GRADUATE SCHOOL

24 July 2020

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Jeffrey M. Brown ENTITLED Effects of Forest Age and Composition on Coleoptera Associated with Fungal Fruiting Bodies in Southwest Ohio BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

Brown, Jeffrey M., M.S., Department of Biological Sciences, Wright State University, 2020. Effects of Forest Age and Composition on Coleoptera Associated with Fungal Fruiting Bodies in Southwest Ohio.

Mature forests often harbor greater biodiversity than younger woods. As this relationship of forest age to biodiversity has not been examined for all taxa, this study sought to document the diversity of mycophilous beetle communities in deciduous forests of southwest Ohio and understand how they vary in relation to forest age. I surveyed fungus associated beetles using baited traps at eight forested sites in the Dayton, Ohio region. Traps were surveyed three times during 2018 to account for seasonal variation, something that has not been done for this geographic region. Forest age had no significant effect on beetle abundance or diversity, but mature forests did have a distinct community of beetles. Invasive honeysuckle had a negative effect on beetle abundance and diversity. With this information, more informed decisions may be made with regard to land use and forest management, maintaining existing mature forests and managing invasive species to enhance biodiversity.

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1. Introduction and Background

1.1 Background

Biodiversity is the sum of all organisms within a specified ecosystem. It includes both flora and fauna, and is usually measured as the total number of species (richness), but species evenness is also useful in characterizing an ecosystem. One cannot fully appreciate the immensity of biodiversity without accounting for insects, which have over one million described species (Stork, 2018). In particular, Coleoptera, which account for at least one third of all described insect species (Zhang et al., 2018), fulfill diverse ecological roles, such as predators, herbivores, fungivores and detritovores.

Greater biodiversity has been found to be associated with more stable and resilient communities that are better able to withstand changes and threats (Hooper et al., 2005). There are many factors that affect biodiversity. Some abiotic factors associated with higher biodiversity are warmer temperatures, higher precipitation, larger contiguous areas of habitat, and geographic isolation (Lövei, 1997). There are biotic factors that can influence community composition as well, such as the proportion of predators and prey, the diversity of vegetation, and invasive species.

Increases in biodiversity within a defined geographical area occur over long periods of time, through speciation and dispersal. Speciation can occur as organisms evolve to exploit different ecological niches more efficiently, and organisms new to the area may colonize through dispersal or migration. In contrast, decreases in diversity can occur rapidly with changing environmental conditions, particular anthropogenically driven ones. These decreases can include local extirpation, or extinction if a species is endemic to a small range, or organisms may migrate to a more suitable habitat if they have high enough mobility. Decreases in biodiversity can lead to lower performance of an ecosystem (Naeem et al., 1994).

Ohio forests have been greatly affected by human influences in the last 150 years. In southwest Ohio, the forests are primarily composed of Sugar Maple (*Acer saccharum*), Oaks (*Quercus* spp.), and to a lesser extent American Beech (*Fagus grandifolia*), American Elm (*Ulmus americana*), and Ash (*Fraxinus* spp.). It has been estimated that Ohio forest cover approached 95% when the first European settlers arrived, but through logging and land clearing for agriculture it was reduced to as low as 10% in the early 1900s. Through land management and shifts in land use, forest cover increased to over 30% by 1994 (ODNR, 2018). Consequently, forests in southwest Ohio may be found in various stages of succession, with very few old growth stands remaining.

Human influence on forest structure in Ohio did not stop with logging. With the accidental introduction of the Emerald Ash Borer, *Agrilus planipennis*, to the United States recorded from Michigan in 2002 (Poland & Mccullough, 2005), the spread to Ohio devastated the Ash trees, potentially permanently changing the forest composition in many areas. This destruction of Ash trees led to an overabundance of coarse woody debris which will persist until it has been fully decomposed. Ohio forests have also been changed by the introduction of Amur honeysuckle (*Lonicera maackii*), which was originally introduced to the United States before 1900 as an ornamental plant and for erosion control, but has since become invasive (Luken & Thieret, 1996).

Mature forests often have an abundance of dead woody debris, as well as fallen leaves and other decaying organic matter which provide an ideal environment for fungi, as moist environments have been shown to increase fungal growth (Osono et al., 2003). Fungal richness is positively correlated with both higher moisture levels in forests and abundance of decaying wood (Pouska et al., 2017). Fungi are heterotrophic, relying on other organisms for their nourishment. The fruiting bodies, or sporocarps, of many fungal species are visible as mushrooms or shelf-like structures on woody material (also known as brackets), with the bulk of the biomass of the organism living inside the substrate as hyphae.

Fungi fill three primary roles in forest ecosystems (Kendrick, 2011). First, they form important symbiotic relationships with plants, increasing the plants' ability to absorb water and nutrients while obtaining nourishment from the plants' photosynthetic products in return. Mycorrhizal fungi and the fungal component of lichens are familiar examples, but endophytic fungi are also found in the living tissues of almost all plants, stimulating plant growth and providing protection from pathogens (Nair & Padmavathy, 2014). The second role filled by fungi is that of parasites or pathogens, such as fungi from the Genus *Armillaria* or the various plant rusts from the Genus *Pucciniales*. The third role is decomposers, or saprotrophs. In this capacity fungi are the primary organisms responsible for the breakdown of cellulose and lignin in decaying plant matter. The boundaries between parasitic and saprotrophic are not always clear, as some fungi may move between roles depending on resource availability (Větrovský et al., 2011). Many saprotrophic fungi rely on dead woody debris, and their fungal sporocarps found near the forest floor provide an important food resource utilized by many organisms.

Fungi are often associated with particular hosts or ecosystems. In forests, fungal diversity is thought to be positively correlated with vascular plant diversity (Rudolf et al., 2013), but there may be other factors, such as disturbance, forest age (Zhiguang et al., 2016), moisture (Zelinka et al., 2020), soil temperature or soil pH (Rousk et al., 2009) that are also important. Greater fungal diversity is beneficial to the decomposition of organic matter on the forest floor.

Detrital foods webs involving fungi are essential to the overall health of the ecosystem through nutrient cycling, returning inaccessible Nitrogen, Phosphorous, Carbon and other minerals to an available state (Attiwill & Adams, 1993). Sporocarps, the fruiting bodies of fungi, are an important food source for many forest animals, both vertebrates and invertebrates. They attract arthropods that use them as a food resource, as well as others seeking a source of prey or hosts to parasitize (Wertheim et al., 2000). Mites, flies, springtails and beetles are the most abundant arthropods found on sporocarps. As most sporocarps are an ephemeral and unpredictable resource, arthropods must have well developed dispersal abilities and a rapid life cycle if they are to use sporocarps as a resource (Ashe, 1981). Coleoptera in particular have been associated with fungi for millions of years, with mycophagy evolving independently within several distinct lineages (Crowson, 1981). Some evidence suggests that relationships between insects and fungus originated as early as the Devonian (Hueber, 2001), and, clear evidence of beetles specializing on fungi can be found in Oxyporine Rove beetles preserved in amber from the Cretaceous (Cai et al., 2017).Some Coleoptera form obligate symbiotic relationships, such as beetles in the subfamily Scolytinae with ambrosia fungi (Vega & Hoftstetter, 2015). Other relationships may be more one sided, with beetles simply using the fungi as a food source, but even in these instances, there is some evidence that feeding behaviors assist in spore dispersal (Lilleskov & Bruns, 2005; Park et al., 2014). Beetles associated with ephemeral sporocarps tend to be generalists, while those associated with persistent sporocarps, such as bracket fungi, may be more specialized. (Põldmaa et al., 2016).

Several studies have sought to characterize the relationship between beetles and fungi, but they are often limited in scope to particular ecosystems or fungal species. For example, Klimaszewski and Peck (1987) found that there is a succession of beetle communities that changes as *Polyporellus squamosus* sporocarps age. Cline and Leschen (2005) created a checklist of beetles found on *Pleurotus ostreatus*, the fungus used as bait in this study.

Several European studies have investigated beetles associated with fungi in coniferous forests. Johansson et al. (2006) found that some rove beetles had a clear preference to the bracket fungi *Fomitopsis pinicola* over other fungal baits. Studying the same fungus, Thunes et al. found a positive relationship of beetle abundance to quantity of coarse woody debris (2000). One European study (Lassauce et al., 2011) found a positive relationship between dead wood volume and species richness of saproxylic beetles, and this relationship was stronger in boreal than temperate forests. Members of the staphylinid genus *Oxyporus*, obligate fungivores, exhibited a wide range of host specificity, ranging from generalist (utilizing fungi from eight families) to exclusively using one species of fungi for their entire life cycle (Hanley & Goodrich, 1995).

Few studies have examined mycophilous beetle communities in Eastern U.S. deciduous forests such as those found in Southwest Ohio. In one of the few studies of fungus-associated beetle communities in Eastern U.S. forests, Epps and Arnold (2010) found that beetle abundance was positively correlated with sporocarp mass, and beetle diversity with sporocarp age.

The various stages of succession of forests in Southwest Ohio provide an opportunity to examine the effects of deciduous forest age on mycophagous Coleoptera diversity and abundance. Understanding this relationship could reinforce the need to preserve the remaining mature forests in Ohio to promote biodiversity.

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1.2 Objectives

Aim 1: The first aim of this study was to document and to quantify the community of mycophilous beetles associated with deciduous forests in southwest Ohio. This was done through systematic trapping.

Aim 2: The second aim of this study was to assess if forest age and composition influence the abundance and diversity of mycophagous beetles. I expected that diversity would be positively correlated with forest age, and that abundance would be positively correlated with volume of coarse woody debris. If older forests are host to a distinct assemblage of beetles, preservation of these habitats and management of invasive honeysuckle will help in the conservation of these species.

2. Research Design and Methods

2.1 Study Area

I surveyed fungus associated beetles in eight old and young forest stands surrounding the greater Dayton area in Southwestern Ohio (Fig. 1). These eights sites (Appendix A) included the Wright State Woods (WSU), as well as Englewood (ENG), Huffman (HUF), Taylorsville (TAY), Germantown (GER), Twin Creek (TWC), Cox Arboretum (COX), and Sugarcreek (SUG) Metroparks. Each was selected as a protected natural area that contained both older and younger forest growth. I obtained a research collecting permit to trap and collect fungus associated beetles from the Five Rivers MetroPark system (Appendix B).

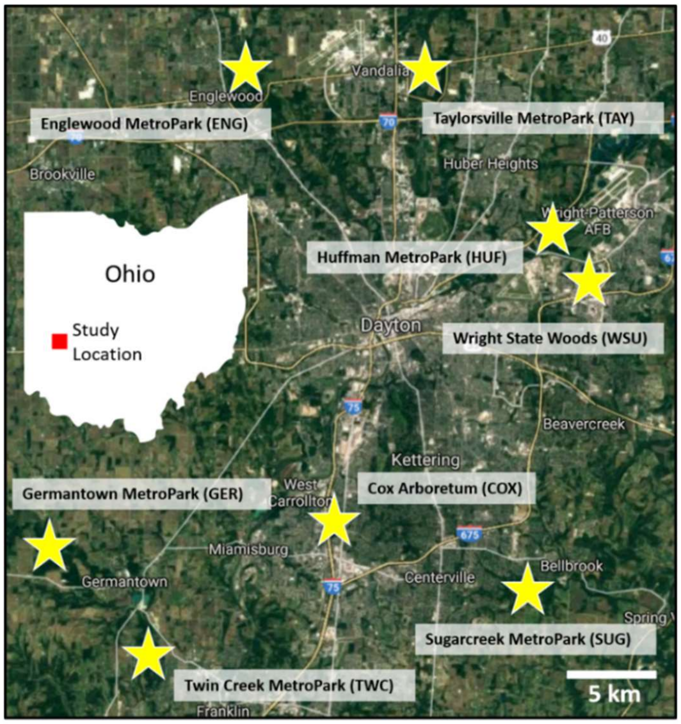


Figure 1. Study sites within the State of Ohio, with Site Abbreviations.

Before going to each park, I examined historical aerial photographs from the Greene (1940) and Montgomery County (1950 – 1960) archives. I selected old forest sites that had well established forest cover in both the historical photographs and the current Google maps satellite view. Taking the latest (1960) date, the older forest sites would be a minimum of 80-100 years old, probably much older as they already appeared established. I selected young forest sites that had little to no forest cover in the historical photographs, but did have forest cover in current Google maps satellite view. I visited each of these sites before setting my traps to verify the site matched the aerial view from Google maps, and that there was still a 40 m transect of woods that was at least 10 m from any trail or edge habitat.

2.2 Study Design

2.2.1 Baited Traps

Figure 2. Cross vane trap.

I constructed small cross vane flight intercept traps (Fig. 2), which were suspended 1 m above the forest floor to minimize disturbance from small mammals. As darker colored traps resemble trees, I used a lighter color to mimic fungi and to reduce bycatch. Traps were baited with commercially available oyster mushrooms, *Pleurotus ostreatus*, a species known to attract a wide variety of mycophagous Coleoptera (Cline & Leschen, 2005). Approximately 10 g of bait was wrapped in cheesecloth, and attached to the trap with a small binder clip, with a non-toxic antifreeze, propylene glycol, placed in the bottom of the trap to be used as a killing agent and preservative. In a preliminary sampling using baited pitfall traps, 9 of 10 were disturbed by wildlife, so this trapping method was not utilized.

2.2.2 Site Layout and Sampling Periods

At each location, I suspended five flight intercept traps in both an older and younger section of forest, for a total of 10 traps per site, 80 traps total. I attempted to select similar flat locations across all sites. The traps were placed 1 m from the forest floor in a straight line, 10 m apart, as much as terrain allowed, and a minimum of 10 m from the edge of the forest to reduce possible edge effects (Figure 3). The old and young sites at Cox Arboretum were the closest in proximity (about 500 m apart), but in most of the other parks the distance was much greater.

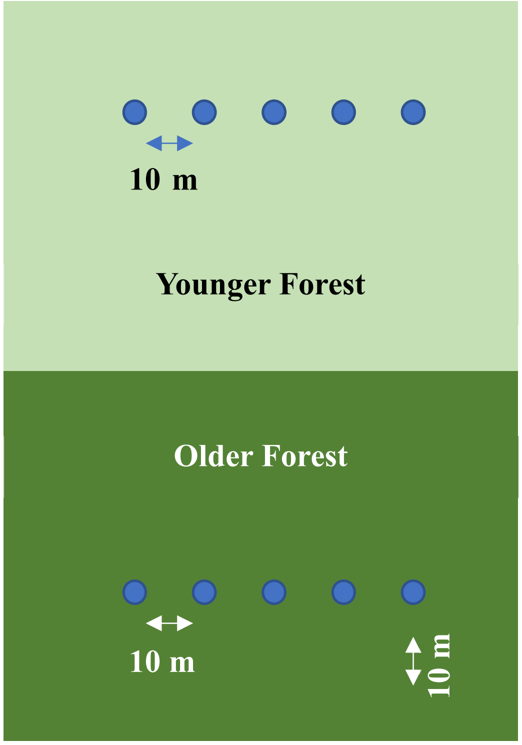


Figure 3. Flight intercept trap placement

As there is known seasonal variation in fungi (North et al., 1997), I sampled each study site three times, once early season (week beginning 4 June 2018, FIRST), once mid-summer (week beginning 23 July 2018, SECOND), and once late season (week beginning 1 October 2018, THIRD). The three dates correspond to late Spring Fungi, Summer fungi and early Fall fungi communities in Southwest Ohio respectively (M.A. Rúa, unpub. data). The same trap locations were used each time in successive sampling periods. Each trap ran for two days, after which I collected all specimens and stored them in sealed bags with a small amount of propylene glycol while in field.

For the third sampling period, the first three trap locations at Huffman MetroPark were destroyed. The trees were cleared by the Miami Conservancy District in area around a water monitoring well. I replaced those three traps in a line continuing past the two remaining undisturbed trap locations.

2.2.3 Processing Samples

Once back in the lab, samples were kept in a freezer until ready for processing. I extracted all Coleoptera from the trap samples and transferred them to vials of 70% ethyl alcohol. I discarded the remaining material, which mostly consisted of Diptera and Hymenoptera. At least one specimen of each morphospecies was pinned or pointed, depending on the size of the specimen, for careful microscopic examination. If I was not sure a specimen matched a previously pinned morphospecies, I pinned it for later comparison.

Specimens were keyed out at least to family using *American Beetles* volumes 1 and 2 (Arnett & Thomas, 2002). As some taxonomy has changed since these were published, I used updated names where available. Specimens were further keyed to genus or species using Arnett & Thomas (2002), or other more current literature when possible. All specimens were assigned to a described species or morphospecies. I was conservative in assigning morphospecies, lumping specimens together if their external morphology, color and size did not present obvious differences. Therefore, true species richness is likely much higher, particularly as some of the very small beetles (< 2 mm) required specialized identification techniques outside the scope of this study, such as dissection. Some of the genera do not have a current dichotomous key.

For analysis, I narrowed the number of specimens by restricting focus to members of families with known fungal associations, according to Arnett & Thomas (2002) and Evans (2014). According to this criterion, 97.6% (2,873/2,943) of trapped beetles belonging to 35 families were retained. Although this overestimates which individual species were associated with fungus, it illustrates that there was a relatively small proportion of bycatch, validating the collection method. All further results and analyses are restricted to this subset of 2,873 beetles from fungal associated families.

2.2.4 Site Characteristics

Using a modified point-quarter method (Cottam & Curtis, 1956), I selected up to 8 trees with a minimum diameter at breast height (DBH) of 10 cm measured 1.5 m from the forest floor, the two trees closest to each trap per quarter, and recorded tree species and DBH. To obtain the estimated tree age, I converted the DBH from cm to inches and multiplied by the estimated growth factor (Appendix C) from Purdue University (Purcell, 2019). Any growth factors not available from Purdue were estimated by comparing similar species and the growth rates from the Morton Arboretum ("Browse Trees and Plants," 2020). I then calculated the average age (using all measured trees) and the average maximum age (using the oldest measured tree per trap) of trees at each site. I did not use estimated mean or maximum tree ages (continuous variables) in my generalized linear mixed models as they were not significantly different than my initial site designations (categorical variable).

To quantify the amount of coarse woody debris (CWD), I walked a 50 m transect along each line of traps. I measured the diameter at each end of all sticks and logs that crossed this transect that were at least 5 cm in diameter. I stopped measuring at 5 m to either side of transect if the CWD continued, and stopped measuring if the diameter went below 5 cm. I estimated the volume by averaging the area of the two ends and multiplying by the length. I then assigned a decay class of 1 - 5 according to Angers et al. (2005). In order to combine the 5 decay classes into one variable for analysis, I weighted each class by their rank and summed the results to give a combined CWD score. The scores were weighted as later stages of wood decay have increased abundance and diversity of fungi (Yuan et al., 2017), potentially attracting a greater abundance and diversity of coleoptera**.**

I quantified the basal area of invasive Amur honeysuckle (HS), *Lonicera maackii*, by measuring the basal stem area of all plants at least 1 cm in diameter in one 5 m x 5 m quarter of each trap, and then summed for the 5 traps at each site.

2.3 Statistical Analysis

All statistical analyses were conducted in *R* 3.6.2 (R Core Team, 2019).

2.3.1 Rarefaction

Once all morphospecies were assigned, I created an overall rarefaction curve with the *iNEXT* package (Hsieh et al., 2020) to determine how well my sampling effort represented the total estimated number of species. I assessed extrapolated values of the rarefaction curve to determine the approximate sampling volume needed to reach the total estimated species in the community. I also examined rarefaction curves separated by old and young woods and separated by sampling period.

2.3.2 Generalized Linear mixed effects models

I used generalized linear mixed effect models with the *lme4* package (Bates et al., 2015) to analyze the effects of my environmental variables on both abundance and richness. Park was assigned as a random effect for all models, as each park likely had other environmental factors that were not recorded which would affect the intercept. Using the *scale* function, I standardized both the honeysuckle and coarse woody debris variables to have their means at zero and to be in units of standard deviations.

As the response variable of abundance was not normally distributed, I used a Poisson error distribution in my model. The optimal model that included my variables of interest had age, season, coarse woody debris, honeysuckle as main effects, with interactions between honeysuckle and age, and honeysuckle and coarse woody debris. This model was arrived at both through manual testing, and using the *step* function to work backwards from a more complex model. This model had a much better fit than the model without interaction terms (ΔAIC = 61.99).

As previous studies (Bock et al., 2007) have shown a strong correlation of richness with abundance, I fit a simple linear model to assess if this pattern held in my data. As my data followed this pattern, I included abundance as a variable in my generalized linear mixed model for richness. The optimal model for richness that included my variables of interest had age, season, coarse woody debris, honeysuckle and abundance as main effects, with no interactions. This model was arrived at both through manual testing, and using the *step* function to work backwards from a more complex model. This simplified model had a better fit than the model with interaction terms (ΔAIC = 3.33). I also fit a generalized mixed model with effective number of species as the response variable.

As the anova summary of generalized mixed models do not directly specify degrees of freedom or P values, I estimated the degrees of freedom by running a linear mixed model, and then calculated a P value from the generalized mixed model F statistic.

For terms with significant interactions, I used the *sjPlot* package (Lüdecke, 2020) to create plots and visualize the strength and direction of these interactions.

2.3.3 NMDS

In order to visualize clustering among sample sites and dates with regard to beetle community composition, I created nonmetric multidimensional scaling (NMDS) plots of the entire data set of fungus associated beetles using the *metaMDS* function from the *vegan* package (Wagner, 2019) in *R*. The input was a site by species abundance matrix of the 48 possible site/age/sampling period variations and the 211 assigned morphospecies. I used the Bray-Curtis dissimilarity and a k value of 4, which provided a reasonable stress value (0.1480) and a high non-metric R^2 (0.978) (Appendix E).

2.3.4 Similarity

To examine similarity of beetle species occurrence between sites and old versus young woods, I calculated Jaccard Indices. I converted my data to binary species presence/absence and the used the *vegdist* function from *vegan* to compute dissimilarity measures, which I then converted to similarities as they are more intuitively understood. I computed the means of Jaccard similarity scores to see if sites were more similar within a park or across age categories. Venn diagrams were created to visualize these similarities and overlap with the package *VennDiagram* (Chen, 2018).

3. Results

3.1 Beetle abundance and richness

In total, the traps collected 2,943 beetles, with 2,873 being potentially fungus associated. There was great variation in the number of beetles found in the 240 individual trap samples. Nine (4%) of the trap samples were disturbed by wildlife, likely deer, raccoons or squirrels, and had no beetles. The number of beetles within individual undisturbed traps ranged from 0 (3 traps from the third sampling period) to 70 (1 trap from first sampling period), with a mean of 12.74 beetles per trap.

I was able to recognize 211 beetle morphospecies (Table 1; Appendix D) from the trap samples, however, as explained in the methods this likely represents an underestimate of species present, particularly for small taxa. My sampling method captured 41% (211 observed / 514 estimated) of the total species estimated to occur in the community as determined by rarefaction (Fig. 4A). In order to capture the total 514 species expected to occur, a much higher sampling effort of approximately 25,000 specimens would be

Table 1. Richness and abundance of Coleoptera by site. Richness totals do not sum, as there are shared morphospecies.

		COX	**ENG**	**GER**	**HUF**	**SUG**	**TAY**	**TWC**	**WSU**	**Total**
Richness	Young	39	22	45	47	35	42	30	23	154
	Old	43	36	22	34	25	36	19	38	128
	Combined	**61**	**50**	**55**	**64**	**52**	**60**	**41**	**53**	**211**
Abundance	Young	282	74	302	307	119	147	169	124	1524
	Old	231	172	140	315	106	128	130	127	1349
	Total	**513**	**246**	**442**	**622**	**225**	**275**	**299**	**251**	**2873**

required. This estimate is restricted to beetles captured by this method, as a suspended flight intercept trap will not capture all beetle taxa.

Overall, my sampling method collected 92% (16.8 observed / 18.3 estimated) of the Shannon effective species (Fig. 4B). Although the young woods appeared to possess higher richness, the old woods sites appeared to harbor a slightly higher number of effective species, indicating that the old woods sites had higher species evenness as indicated by the Simpson diversity index (Table 2).

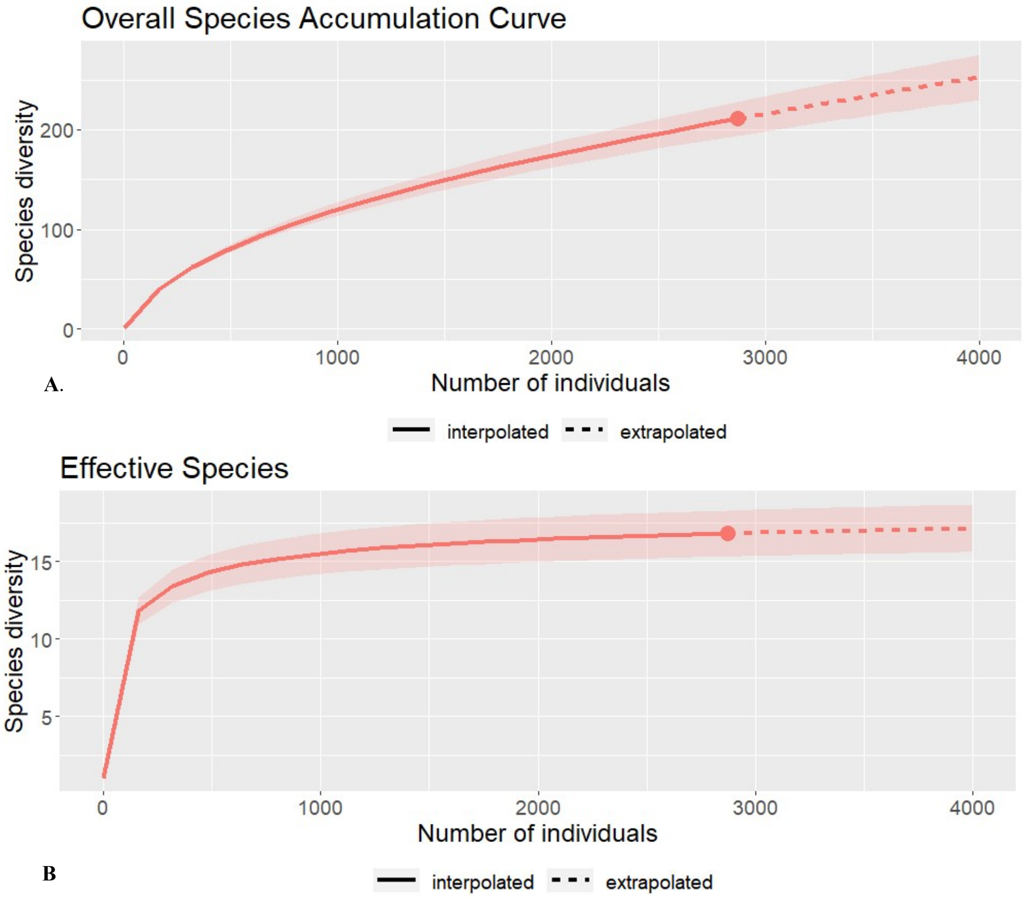


Figure 4. Species accumulation curves for total species (**A**) and effective species (**B**) for entire season and across all sites.

Table 2. Diversity indices separated by age and season. The estimated values are from rarefaction, with the standard error (s.e.), along with a 95% CI, lower confidence level (LCL) and upper confidence level (UCL). Shannon and Simpson diversity indices are converted to effective species.

	Diversity	Observed	Estimated	s.e.	LCL	UCL
Total	Species richness	211	515	89.3	384	745
	Shannon diversity	16.8	18.3	0.7	16.8	19.7
	Simpson diversity	5.4	5.4	0.2	5.4	5.8
Young	Species richness	154	318	51.5	244	453
	Shannon diversity	15.4	17.1	0.9	15.4	18.9
	Simpson diversity	5.0	5.0	0.2	5.0	5.4
Old	Species richness	128	260	47.9	194	391
	Shannon diversity	16.1	17.7	1.0	16. 1	19.7
	Simpson diversity	5.8	5.8	0.3	5.8	6.3
First	Species richness	124	328	77.8	223	544
	Shannon diversity	17.3	19.6	1.1	17.4	21.8
	Simpson diversity	7.5	7.6	0.3	7.5	8.2
Second	Species richness	95	269	75.531	172	488
	Shannon diversity	9.4	10.5	0.7	9.4	11.9
	Simpson diversity	3.8	3.8	0.2	3.8	4.1
Third	Species richness	53	174	84.9	88	471
	Shannon diversity	6.5	7.3	0.7	6.5	8.7
	Simpson diversity	2.5	2.5	0.2	2.5	2.8

The five dominant families by abundance (Latridiidae: 1,112, Curculionidae: 614, Cleridae: 306, Mordellidae: 254, Staphylinidae: 219) composed 85% of individuals collected, with Latridiidae alone composing 38% (Figure 5a). The family rankings for species richness were quite different than for abundance, with a somewhat more even distribution. There were 35 families present, with the five dominant families by species richness (Staphylinidae: 45, Mordellidae: 24, Elateridae: 20, Curculionidae: 19, Nitidulidae: 16) composing 58% of species collected, with Staphylinidae alone composing 21% (Figure 5b).

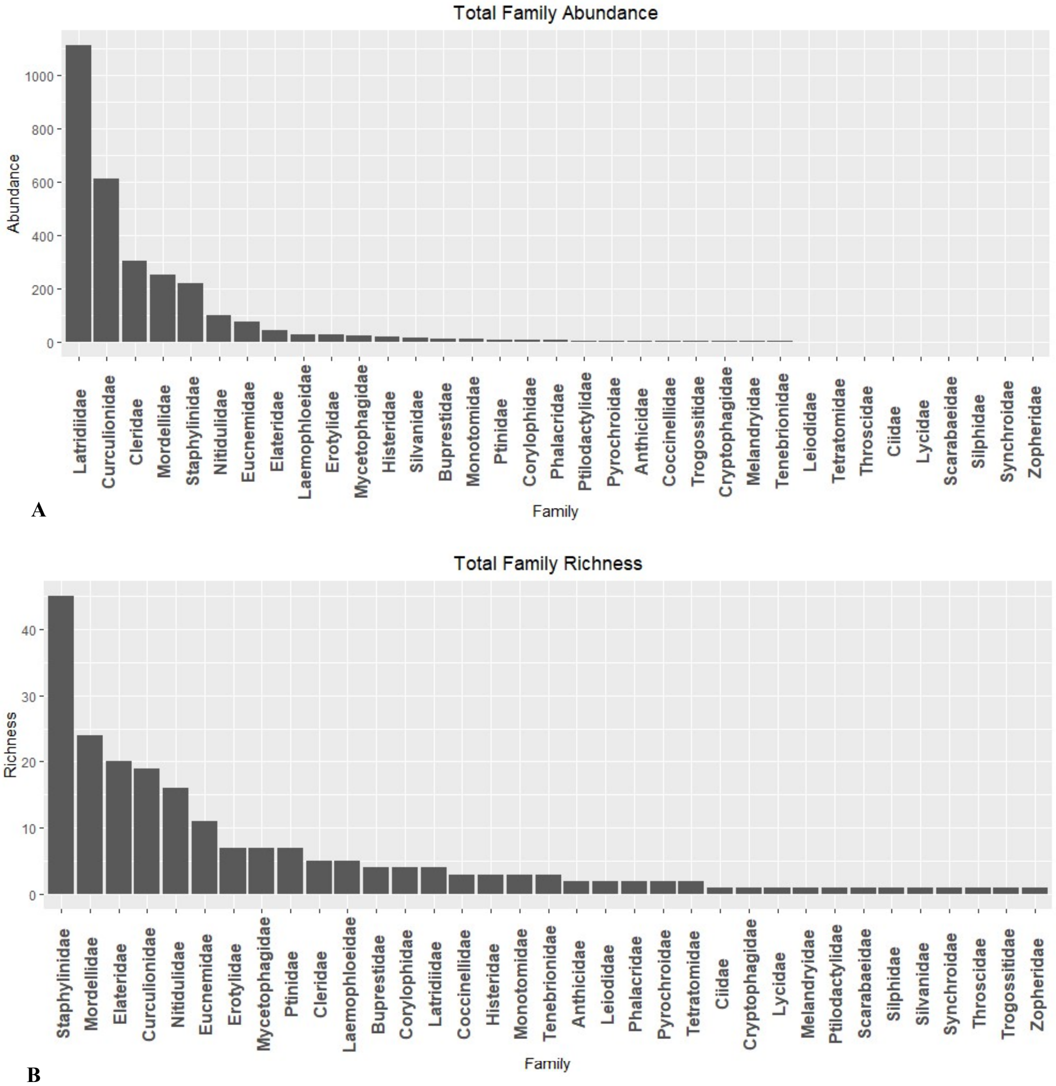


Figure 5: Total abundance (**A**) and richness (**B**) per family across all traps and sampling periods

3.2 Effects of Forest Age

3.2.1 Site Characteristics

Comparing my site designations of old and young woods to my estimated tree ages (Table 3) provided support for my division, as only one site (ENG) and two sites (ENG and SUG) did not match my designation when comparing the average maximum age, and average age respectively. The young Englewood site had several large relic Osage orange trees which skewed the age of that fragment.

Table 3. Estimated **a**verage age and average maximum age of trees in years **at each site. Sites where the Old was not greater than young are indicated with (*).**

Park	Site	Average Max Age	Average Age
COX	**Old**	109	63
	Young	69	47
ENG	**Old**	98*	58*
	Young	126	65
GER	**Old**	91	81
	Young	80	55
HUF	**Old**	171	92
	Young	140	57
SUG	**Old**	104	47*
	Young	71	66
TAY	**Old**	122	69
	Young	76	48
TWC	**Old**	114	75
	Young	100	64
WSU	**Old**	118	80
	Young	73	52

In examining coarse woody debris (Figure 6) with paired t-tests, there was no statistically significant difference between the old and young woods based on total volume (t = -0.7184, df = 7, *P* = 0.4958) or volume weighted by decay class (t= -0.7254, df = 7, *P* = 0.4918). Decay classes 3 and 4 were the most common, together comprising 79.8% of the recorded volume, with decay class 1 (freshly fallen) being scarce, only representing 0.7% of the recorded volume. The Sugarcreek MetroPark young woods site had a very high volume of downed wood, which appeared to be ash based on the distinctive larval emerald ash borer galleries.

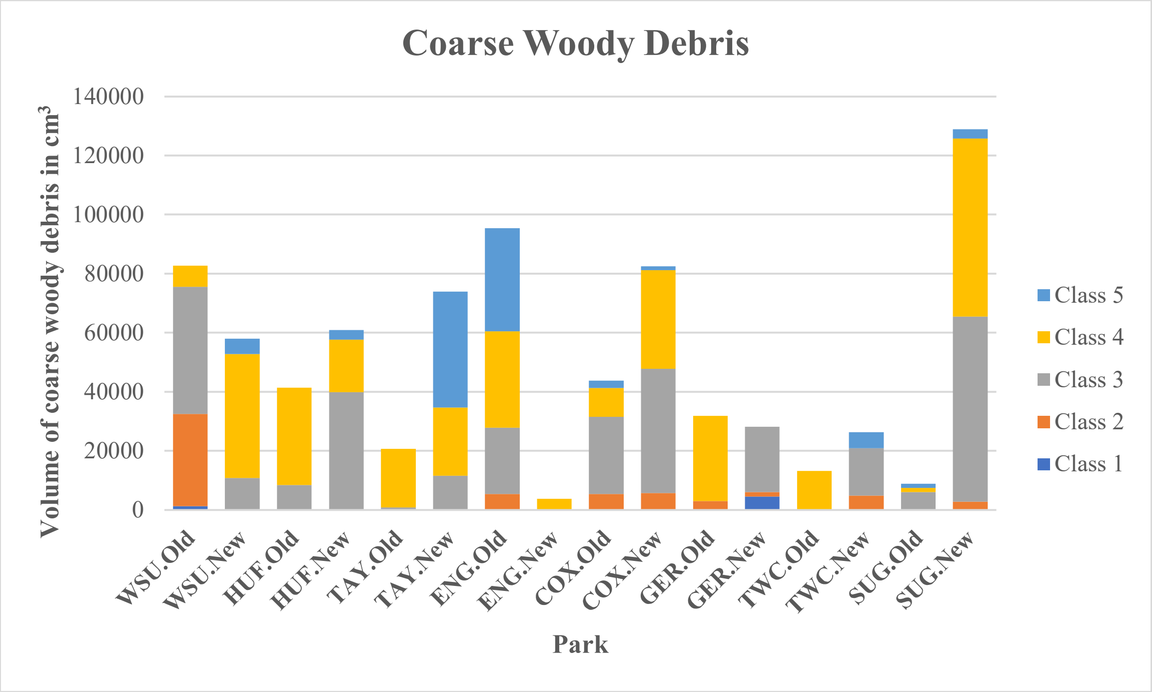


Figure 6. Decay class and volume in cm^3 of coarse woody debris, separated by park and forest age

3.2.2 Abundance

My optimal generalized linear mixed model to explain beetle abundance had park as a random effect with age, season, coarse woody debris and honeysuckle as fixed effects, and included the interactions between age and honeysuckle, and between coarse woody debris and honeysuckle. Beetle abundance significantly declined over the season ($F_{2,33}$= 103.822, *P* = 5.6e-15) and with increasing honeysuckle ($F_{1,24}$ = 13.936, *P* = 0.001; Table 4; Appendix F). The older woods also exhibited lower beetle abundance ($F_{1,38}$= 11.704, *P* = 0.002). Coarse woody debris showed a negative trending but not significant effect in the glm model (*P* = 0.113), though the ANOVA model summary indicated a significant effect ($F_{1,24}$ = 9.853, *P* = 0.005). This discrepancy may be due to error in the estimated degrees of freedom.

Table 4: Anova table of generalized mixed model for abundance, including coarse woody debris (CWD) and honeysuckle (HS).

	Num. df	**Den. df**	**F value**	***P***
Age	1	37.879	11.7035	0.0015
Season	2	33.075	103.8217	5.553e-15
CWD	1	23.677	9.8527	0.0045
HS	1	24.087	13.9359	0.0010
Age * HS	1	22.670	47.5021	5.418e-07
CWD * HS	1	12.567	17.1148	0.0013

Although honeysuckle had a negative effective on abundance, looking at the interactions, this effect was ameliorated by both volume of coarse woody debris and age of the forest.

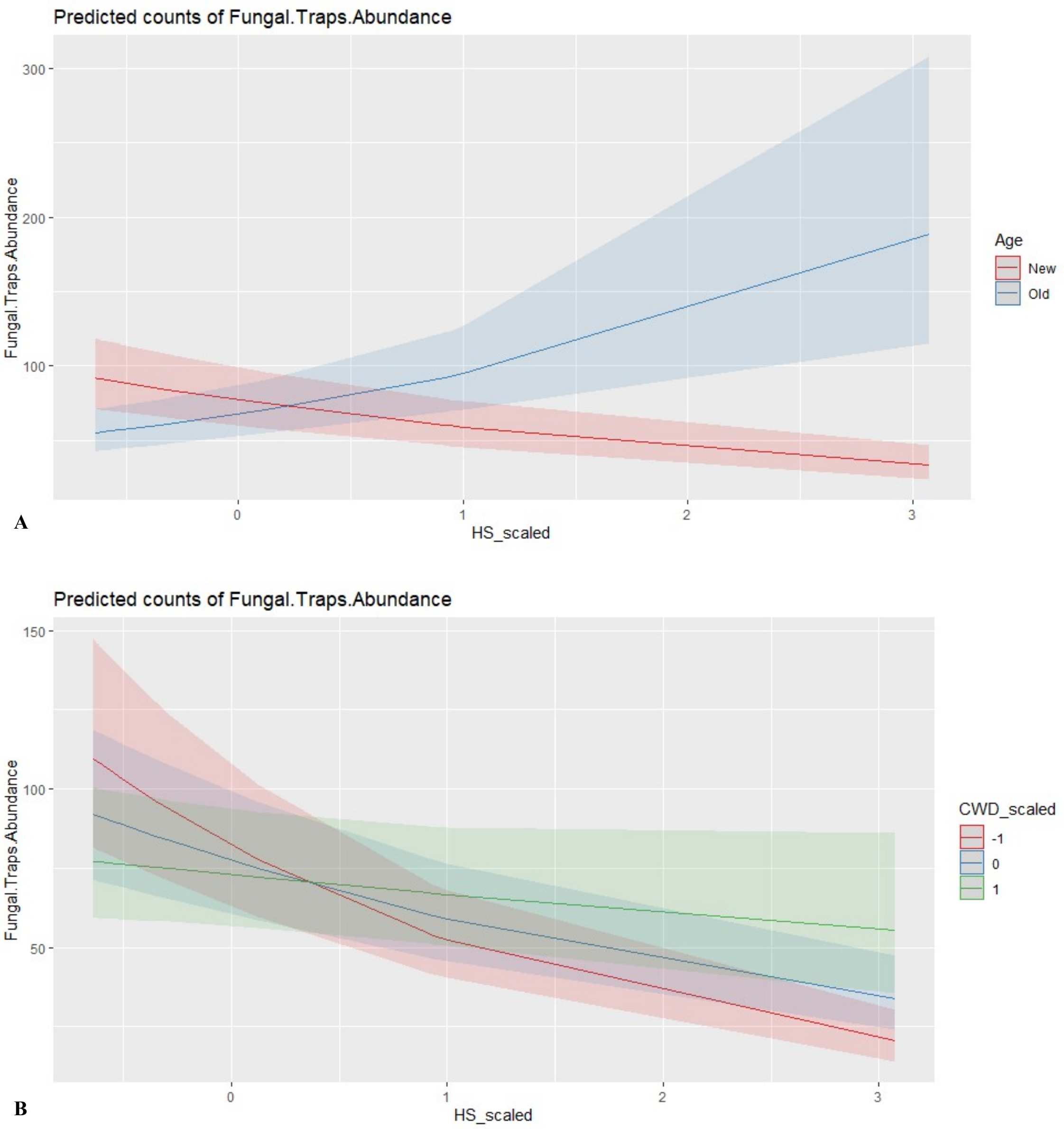


Figure 7. Interaction plots showing effect on abundance of honeysuckle between old and new forests (**A**), and with increased volume of coarse woody debris (**B**). Abundance is number of beetles, coarse woody debris (CWD) and honeysuckle (HS) have been scaled into standard deviations with their means centered at zero.

3.2.3 Richness

As expected, species richness had a strong positive correlation with abundance (P = 2.1e-06), but with a relatively low adjusted R^2 (0.38), other environmental variables accounted for much of the variation (Figure 8).

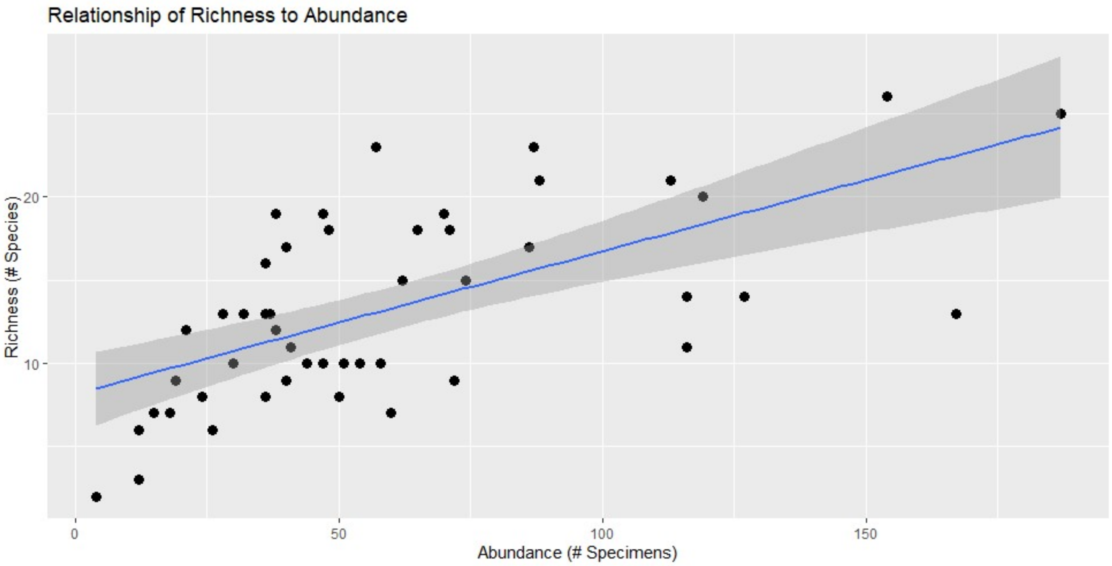


Figure 8. Relationship of species richness to species abundance. The blue line is regression from a simple linear model with the shaded area representing S.E.. Each dot corresponds to one sampling period for a set of traps.

My optimal generalized linear mixed model to explain richness had age, season, coarse woody debris, honeysuckle and abundance as fixed effects, with park as a random effect. Beetle species richness declined over the season ($F_{2,36}$ = 23.2277, P = 3.3e-07), and with increasing honeysuckle ($F_{1,20}$ = 7.8669, P = 0.0109; Table 5; Appendix F). Richness tended to be greater in young woods, but this was not significant ($F_{1,39}$ = 1.8914, P = 0.1768). Coarse woody debris had a marginally non-significant positive effect on richness ($F_{1,34}$ = 3.3622, P = 0.0757).

In contrast to richness, the effective number of species showed almost no correlation with abundance (*P* = 0.839). A linear mixed model with effective number of species as the response variable only recovered season as a significant effect ($F_{2,34} = 8.713$, *P* = 0.001).

Table 5: Anova table of generalized mixed model for richness

	Num. df	**Den. df**	**F value**	***P***
Age	1	39.731	1.8914	0.1768
Season	2	35.939	23.2277	3.3498e-07
CWD	1	33.526	3.3622	0.0757
HS	1	20.112	7.8669	0.0109
Abundance	1	32.314	14.2259	0.0007

3.3 Effect of season

Species richness did not significantly differ between old and young woodlands, but richness showed a marked linear decline over the second and third sampling periods (Figure 9a). Abundance was similar over the first two sampling periods, but dropped significantly in the third sampling period (Figure 9b).

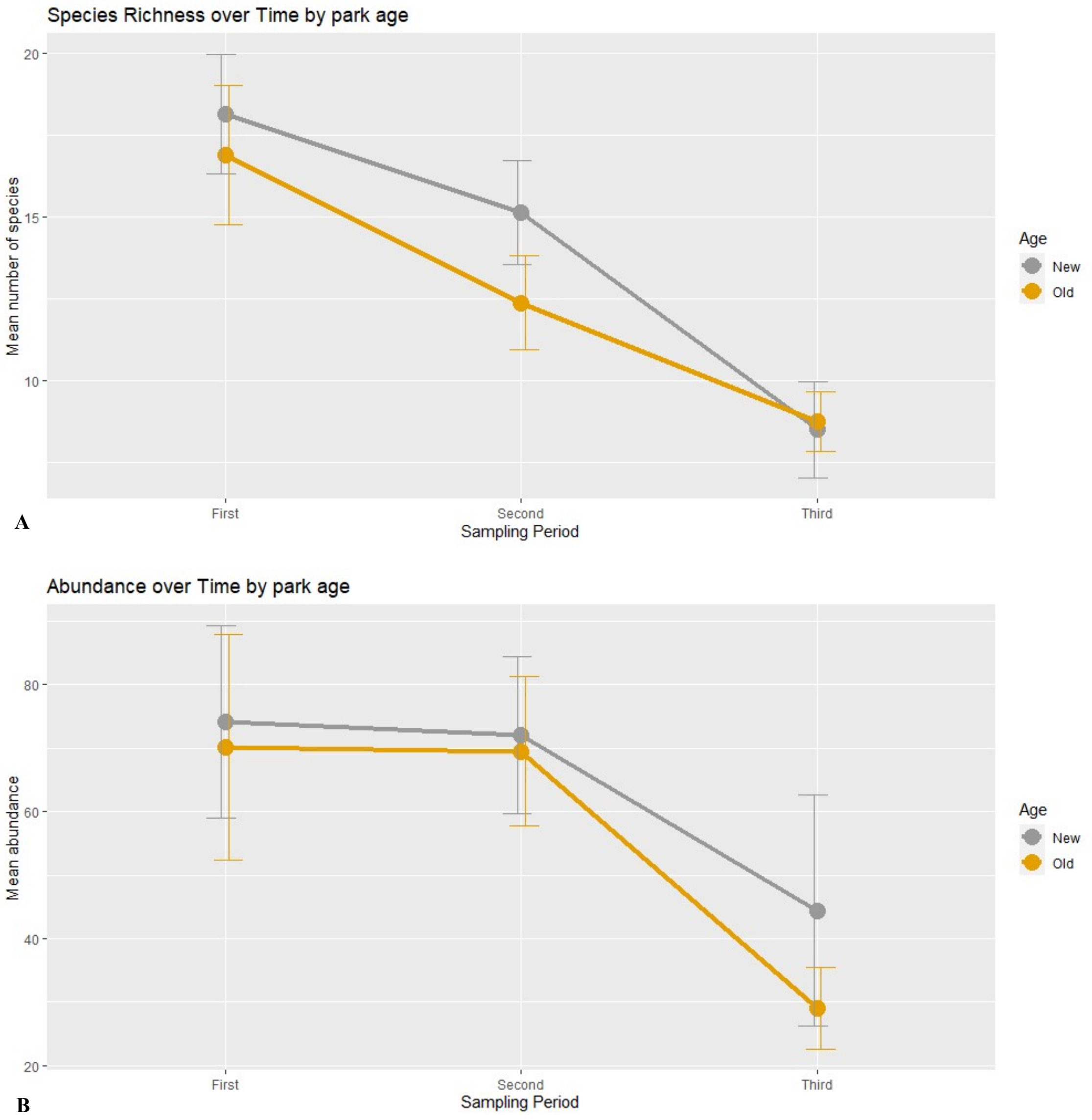


Figure 9. Mean beetle richness (**A**) and abundance (**B**) per site with S.E. over season separated by age.

NMDS ordination of sampling sites by sampling period did not reveal clear clustering of trap samples based on geographic site (Figure 10a) or forest age (Figure 10b). However, when separated by sampling period, there was a clear pattern with little overlap (Figure 10c).

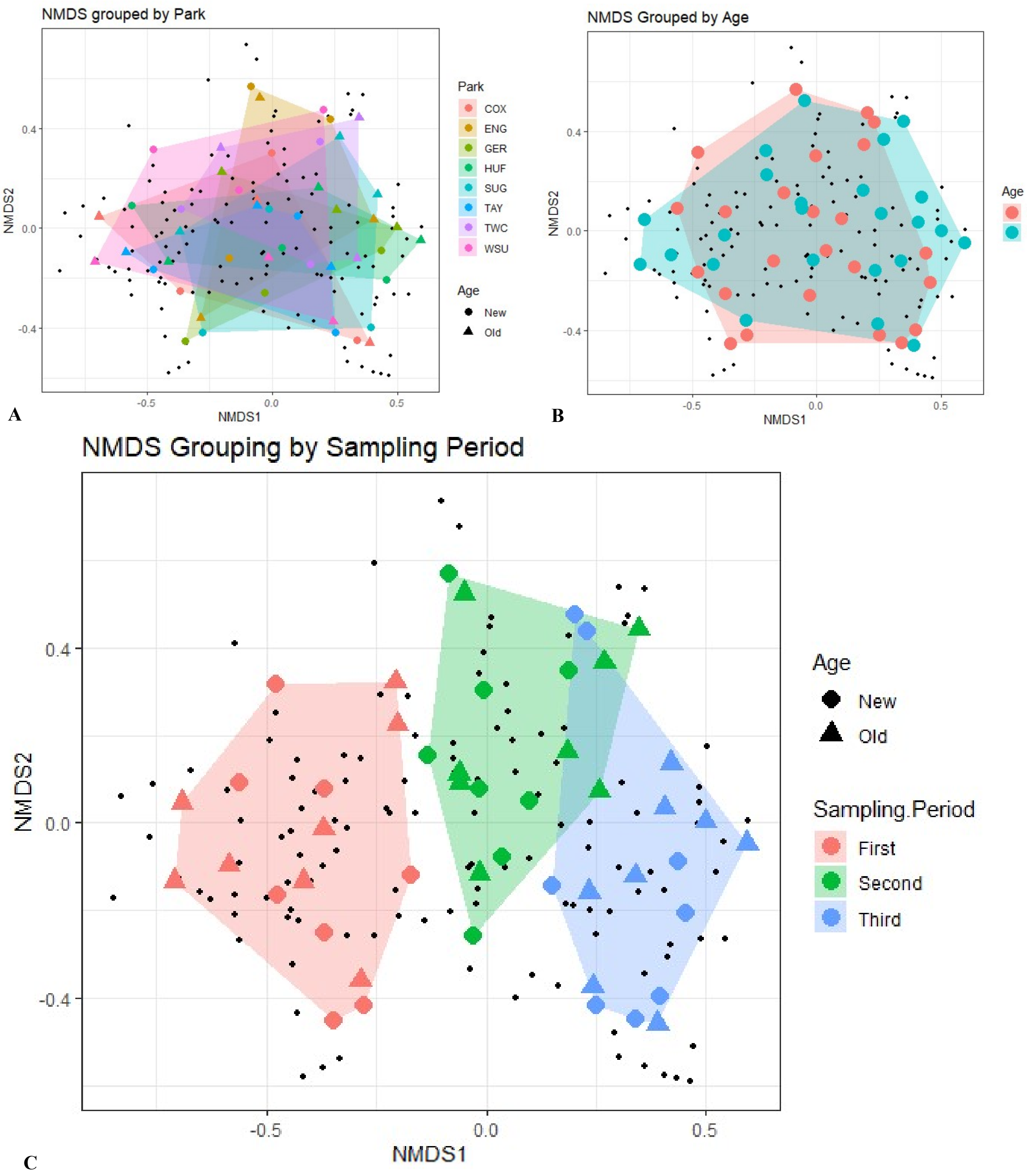


Figure 10. NMDS of samples grouped by park (**A**), age (**B**) and sampling period (**C**). Small dots represent beetle morphospecies.

The overall Jaccard similarity between the old and young woods was 0.34. Of the 211 morphospecies, 83 were unique to the young woods, 57 were unique to the old woods, and 71 were shared (Figure 11).

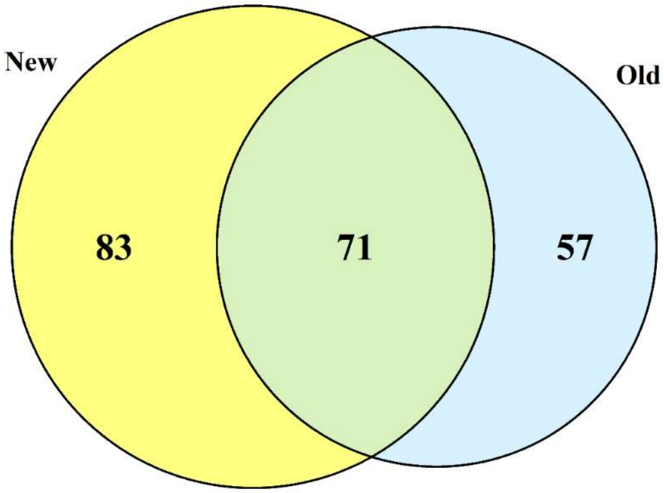


Figure 11. Species overlap between old and young sites

Jaccard similarities between sites and between old and young woods are shown in Table 6. On average, the Jaccard similarity for Old/Young within a park was the highest (0.23, s = 0.08), followed by measures between parks, Old/Old (0.20, s = 0.05), Young/Old (0.19, s = 0.06) and Young/Young (0.17, s = 0.06), with a maximum of 0.34 and a minimum of 0.07.

Table 6. Jaccard similarity index for all sites. The shaded cells are a comparison between young and old of the same park. Values above represent comparison of young (row) to old (column). Values below represent comparison of young to young.

	COX	**ENG**	**GER**	**HUF**	**SUG**	**TAY**	**TWC**	**WSU**
COX	0.34	0.19	0.17	0.26	0.21	0.23	0.16	0.28
ENG	0.09	0.16	0.19	0.10	0.12	0.16	0.17	0.07
GER	0.24	0.14	0.22	0.22	0.19	0.25	0.14	0.26
HUF	0.26	0.10	0.28	0.27	0.20	0.22	0.12	0.23
SUG	0.23	0.12	0.16	0.15	0.15	0.15	0.13	0.20
TAY	0.21	0.12	0.23	0.25	0.13	0.32	0.13	0.29
TWC	0.19	0.11	0.15	0.15	0.18	0.14	0.20	0.17
WSU	0.17	0.15	0.13	0.15	0.07	0.23	0.10	0.15

There were only 12 morphospecies (5.7%) collected in all 3 sampling periods (Figure 12). The first and second sampling periods were the most similar, sharing 40 morphospecies (22.4%), and the first and third sampling periods were the least similar, only sharing 16 morphospecies (9.9%).

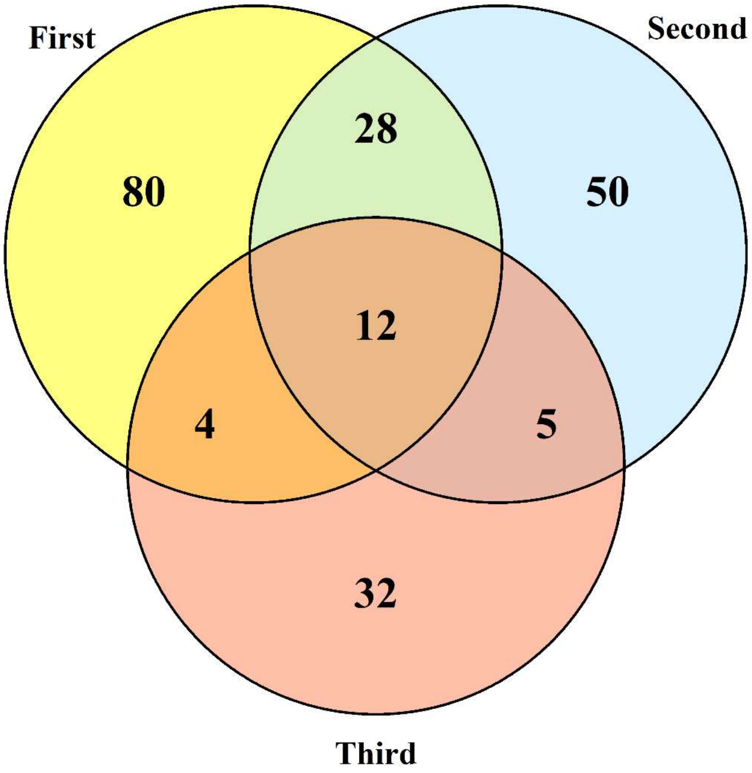


Figure 12. Species overlap between sampling periods

4. Discussion

4.1 Fungus associated beetle communities in Southwest Ohio woodlands

One of the first things that stands out from this study is the great diversity of beetles captured. With a conservative 211 morphospecies assigned and an estimated 515 species that could be captured by this method, this sampling effort was just a beginning in documenting fungus-associated beetles in southwest Ohio. As mentioned earlier, my methods may have underestimated the total number of beetle species but overestimated the number of species that were associated with fungi, as many beetles have diverse feeding preferences, even within a family.

Interestingly, the beetle genus *Melanophthalma* (Latridiidae) was captured with the by far the greatest abundance (1,106), but is not known to be associated with the fungal bait utilized in this study, *Pleurotus ostreatus* (oyster mushrooms) (Cline & Leschen, 2005). These beetles normally feed on fungal spores from different families of fungi and are typically collected from leaf litter. They may have used the scent of the oyster mushrooms to locate decaying wood, which might be suitable for their preferred fungi as well. A closely related genus of Latridiidae, *Corticarina*, has been associated with oyster mushrooms. Although the family Latridiidae had the highest abundance, it had low diversity, with only four recognized morphospecies. This may be an accurate assessment, or simply an artifact of my conservative assignment of morphospecies. A closer examination by a latridiid expert might reveal many more species that are superficially similar in morphology.

Neither of the next two most abundantly collected taxa, *Xyleborus* sp. (Curculionidae, 486 specimens) and *Pyticeroides laticornis* (Cleridae, 188 specimens), have known direct associations with oyster mushrooms. They are directly associated with each other though, as *P. laticornis* is a known predator of *Xyleborus*, and both are attracted to the semiochemical conophthorin. This compound was originally thought to originate only from plants, but is now known to be released from fungi as well (Zhao et al., 2019).

Over half of the recognized morphospecies were singletons, which may give a false impression of the dissimilarity in beetle composition among sites. A greater sampling effort may find more specimens at other sites, or possibly, many of these species are relatively rare. Sampling over several seasons would provide more complete coverage and beetle phenology.

I expected a greater abundance of species belonging to families with direct, obligate fungal relationships, such as Cryptophagidae, Erotylidae, Mycetophagidae and Tetratomidae. All were present, but in low quantities. I have personally collected Erotylidae frequently from oyster mushrooms, but perhaps the height of the trap from the ground (1 m) discouraged some taxa, or a greater volume of bait would be needed. Other taxa of very small mycophagous beetles, such as Leiodidae, feed on subterranean fungi (Kodada et al., 2019) and would not be expected very high from the ground.

According to my models, both fungus associated beetle abundance and richness were negatively correlated with increased presence of Amur honeysuckle (*Lonicera maackii*). It is not clear if this is a causative relationship, or simply correlation, but honeysuckle has been shown to negatively affect both native vascular plant communities (Dorning & Cipollini, 2006) and the abundance of mycorrhizal fungi (Shannon et al., 2014). Discerning the nature of the effects of honeysuckle on the fungus associated beetle community would require a carefully controlled longitudinal study over several years, as the effects of adding or removing honeysuckle are not immediately manifest. Honeysuckle has been shown to discourage seedlings of native trees (Gorchov & Trisel, 2001), which would alter the forest composition as older trees die without replacement. In the long term, this would reduce the suitable habitat for many fungus associated beetles. It is also possible that the increase in honeysuckle is a positive response to some other existing variable, such as disturbance, which is already unfavorable to fungus associated beetles.

There was no support for my hypothesis that older forests would have greater diversity of fungus associated beetles. In contrast, there was a trend in the opposite direction with younger forests having a greater species richness ($P = 0.058$). This could be due to environmental factors not accounted for in this study, such as degree of disturbance or moisture levels. If forests were selected with a greater difference in age, and an increment borer was used to more accurately assess mean and maximum tree age, a finer resolution of the effect of forest age might be obtained by using age as a continuous instead of categorical variable. I had also expected there to be a higher volume of coarse woody debris in the older forests, which has been shown to have a positive effect on coleopteran richness (Lassauce et al., 2011), but this pattern was not observed in this study.

Neither was there support for my hypothesis that the abundance of fungus associated beetles would be associated with a greater amount of coarse woody debris, although an increased volume of coarse woody debris appeared to help mitigate the negative effect of honeysuckle. Perhaps the higher volumes of coarse woody debris helped provide a suitable substrate for fungal growth where it would not normally have occurred in the presence of honeysuckle.

Season (sampling period) was the most significant variable in determining beetle community composition, consistent with previous studies of Coleoptera (Castro et al., 2013) and Lepidoptera (Stireman, et al., 2014; Summerville & Crist, 2003). The final sampling period during the first week of October was significantly lower in both abundance and richness. This may have been due to low precipitation in the weeks previous to the sampling period, which is known to affect the abundance of sporocarps (Genevieve et al., 2019; Straatsma et al., 2001).

There are plenty of opportunities left to expand our knowledge of mycophagous beetles in Southwest Ohio. Using the same type of traps and bait over the full season instead of only three discrete trapping events would capture a greater number of species, and perhaps more interestingly show the changes in seasonal abundance of various taxa. A different species of fungus could also be used which might attract a different set of beetles. Baited pitfall traps would also capture a different assemblage of beetles, as some stay close to the forest floor, and feed on subterranean fungal sporocarps. Perhaps one of the best ways would be active sampling of sporocarps. This would be labor intensive, but have the benefits of direct beetle – fungal host association and very little bycatch.

4.2 Conclusion

There are many challenges to preserving the diversity of mycophagous Coleoptera and their associated foodwebs. Even though my results do not show a higher abundance or diversity of mycophagous beetles in older forest around the Dayton, Ohio area, they do suggest that the identity of beetle species may differ from that of the younger woods. Preserving the remaining contiguous areas of older growth forests intact will likely help to maintain and encourage biodiversity in the region, although it also appears important to maintain younger aged forest tracts as well. Removal of invasive honeysuckle will likely benefit the beetle community with no otherwise ill effects, other than being labor intensive. The success of the beetles is likely directly tied to the success of their fungal hosts, which can be affected by many environmental variables. Some beetles associated with fungi may have to adapt to changing climate as well, as there is support for warmer temperatures altering fungal fruiting times (Kauserud et al., 2008).

Acknowledgements

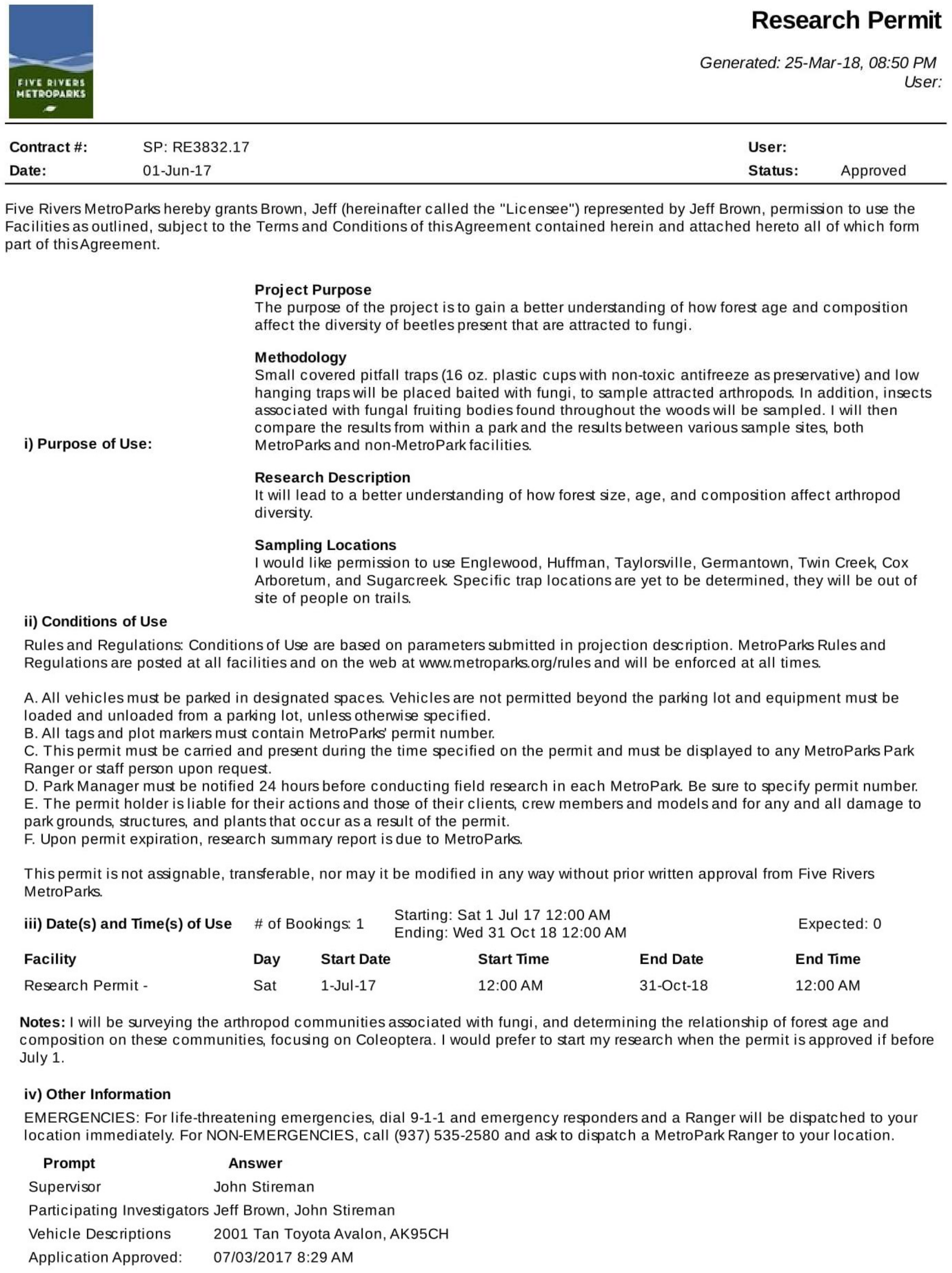
I would like to thank my family for supporting me during all the time spent away from home working on this project, my daughter Anna was especially helpful, often acting as my scribe while in the field. Dr. Stireman and his lab were always supportive and helped me to translate my ideas into scientific writing. Dr. Bahn was a great resource for statistics, and Dr. Rúa for fungi. BugGuide.net and the Ohio Coleopterists were both instrumental in assisting with identifications and my desire to study beetles.

Appendix

Appendix A: GPS Coordinates for study locations

		Latitude	Longitude
Cox Arboretum	**Young**	39.6542	-84.2290
	Old	39.6579	-84.2319
Englewood	**Young**	39.8809	-84.2825
	Old	39.8876	-84.2854
Germantown	**Young**	39.6355	-84.4081
	Old	39.6410	-84.4218
Huffman	**Young**	39.7995	-84.0908
	Old	39.7998	-84.0873
Sugarcreek	**Young**	39.6184	-84.0979
	Old	39.6239	-84.0958
Taylorsville	**Young**	39.8733	-84.1614
	Old	39.8872	-84.1558
Twin Creek	**Young**	39.5743	-84.3528
	Old	39.5943	-84.3537
WSU	**Young**	39.7861	-84.0521
	Old	39.7803	-84.0560

Appendix B: MetroParks Collecting Permit



Research Permit

Generated: 25-Mar-18, 08:50 PM
User:

Contract #:	SP: RE3832.17	**User:**	
Date:	01-Jun-17	**Status:**	Approved

Five Rivers MetroParks hereby grants Brown, Jeff (hereinafter called the "Licensee") represented by Jeff Brown, permission to use the Facilities as outlined, subject to the Terms and Conditions of this Agreement contained herein and attached hereto all of which form part of this Agreement.

i) Purpose of Use:

Project Purpose
The purpose of the project is to gain a better understanding of how forest age and composition affect the diversity of beetles present that are attracted to fungi.

Methodology
Small covered pitfall traps (16 oz. plastic cups with non-toxic antifreeze as preservative) and low hanging traps will be placed baited with fungi, to sample attracted arthropods. In addition, insects associated with fungal fruiting bodies found throughout the woods will be sampled. I will then compare the results from within a park and the results between various sample sites, both MetroParks and non-MetroPark facilities.

Research Description
It will lead to a better understanding of how forest size, age, and composition affect arthropod diversity.

Sampling Locations
I would like permission to use Englewood, Huffman, Taylorsville, Germantown, Twin Creek, Cox Arboretum, and Sugarcreek. Specific trap locations are yet to be determined, they will be out of site of people on trails.

ii) Conditions of Use

Rules and Regulations: Conditions of Use are based on parameters submitted in projection description. MetroParks Rules and Regulations are posted at all facilities and on the web at www.metroparks.org/rules and will be enforced at all times.

A. All vehicles must be parked in designated spaces. Vehicles are not permitted beyond the parking lot and equipment must be loaded and unloaded from a parking lot, unless otherwise specified.
B. All tags and plot markers must contain MetroParks' permit number.
C. This permit must be carried and present during the time specified on the permit and must be displayed to any MetroParks Park Ranger or staff person upon request.
D. Park Manager must be notified 24 hours before conducting field research in each MetroPark. Be sure to specify permit number.
E. The permit holder is liable for their actions and those of their clients, crew members and models and for any and all damage to park grounds, structures, and plants that occur as a result of the permit.
F. Upon permit expiration, research summary report is due to MetroParks.

This permit is not assignable, transferable, nor may it be modified in any way without prior written approval from Five Rivers MetroParks.

iii) Date(s) and Time(s) of Use # of Bookings: 1 Starting: Sat 1 Jul 17 12:00 AM Ending: Wed 31 Oct 18 12:00 AM Expected: 0

Facility	Day	Start Date	Start Time	End Date	End Time
Research Permit -	Sat	1-Jul-17	12:00 AM	31-Oct-18	12:00 AM

Notes: I will be surveying the arthropod communities associated with fungi, and determining the relationship of forest age and composition on these communities, focusing on Coleoptera. I would prefer to start my research when the permit is approved if before July 1.

iv) Other Information

EMERGENCIES: For life-threatening emergencies, dial 9-1-1 and emergency responders and a Ranger will be dispatched to your location immediately. For NON-EMERGENCIES, call (937) 535-2580 and ask to dispatch a MetroPark Ranger to your location.

Prompt	Answer
Supervisor	John Stireman
Participating Investigators	Jeff Brown, John Stireman
Vehicle Descriptions	2001 Tan Toyota Avalon, AK95CH
Application Approved:	07/03/2017 8:29 AM

Appendix C: Tree Growth Factors

Growth Factor x DBH in inches gives a rough estimate of tree age

	Growth Factor
American Basswood	3
American Beech	6
American Elm	4
Bitternut Hickory	7.5
Black Cherry	5
Black Locust	3
Black Walnut	4.5
Blue Ash	5
Chestnut Oak	5.5
Chinkapin oak	6
Cottonwood	2
Eastern Red Cedar	4
Hackberry	3.5
Honey Locust	3
Northern Red Oak	4
Ohio Buckeye	5
Osage Orange	4
Shagbark Hickory	7.5
Sugar Maple	5.5
Sycamore	4
White Oak	5

Appendix D: Alphabetical list of species and morphospecies by family

☐ Genus or Species determined 🟩 Morphospecies assigned

Family	Genus	Species	Quantity
Anthicidae			
	Anthicus	*cervinus*	1
	Notoxus	*NotoOne*	4
Buprestidae			
	Agrilus	*MedGold*	2
	Agrilus	*NotEAB*	1
	Agrilus	*ProKeel*	3
	Agrilus	*Small DarkGreen*	7
Ciidae			
		SmallHorns	1
Cleridae			
	Cregya	*mixta*	1
	Cymatodera	*bicolor*	1
	Enoclerus	*nigripes*	1
	Madoniella	*dislocata*	115
	Pyticeroides	*laticornis*	188
Coccinellidae			
	Brachiacantha	*quadripunctata*	1
	Microweisea	*TinyTiny*	2
	Scymnus	*HairyRound*	1
Corylophidae			
	Holopsis	*ClearFront*	2
	Orthoperus	*TooSmall*	3
	Sericoderus	*lateralis*	1
		Small Hooded	1
Cryptophagidae			
	Cryptophagus	*ProCircle*	3
Curculionidae			
	Conotrachelus	*anaglypticus*	1
	Cyrtepistomus	*castaneus*	1
	Dryophthorus	*americanus*	7
	Oedophrys	*hilleri*	2
	Phloeotribus	*PseudoClub*	3
	Scolytus	*Scoly FlatHead*	6
	Stenoscelis	*brevis*	4
	Xyleborus	*Scoly One*	486
		Bigeye tucknose	12
		HairySmall	4
		Notch Tucknose	4
		Scoly FlatClub	2
		Scoly Medium	4
		Scoly Skinny	36
		Scoly Tiny	30
		ScolyLong	1

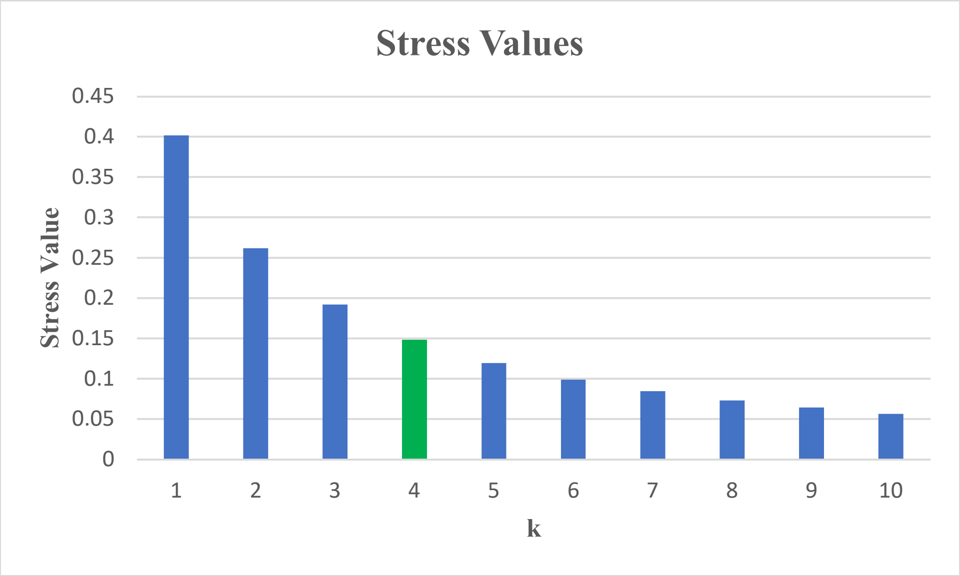
		Smalleye Tucknose	2
		WhiteCenter	1
Elateridae			
	Ampedus	*areolatus*	3
	Ampedus	*HairyBall*	3
	Ampedus	*nigricollis*	1
	Ampedus	*semicinctus*	1
	Athous	*LongNotum*	8
	Glyphonyx	*CurveAngle*	7
	Hemicrepidius	*BigBoy*	1
	Horistonotus	*curiatus*	1
	Idolus	*Nondescript*	3
	Lacon	*discoideus*	1
	Melanotus	*BlackLong*	1
	Melanotus	*BrownChopped*	1
		Constricted	3
		Edges	1
		GoldStraight	1
		HairyPaleEdge	1
		LongHair	1
		Straight	2
Erotylidae			
	Acropteroxys	*gracilis*	1
	Dacne	*quadrimaculata*	1
	Glischrochilus	*sanguinolentus*	1
	Toramus	*pulchellus*	1
	Triplax	*festiva*	1
	Triplax	*flavicollis*	19
	Triplax	*thoracica*	3
	Tritoma	*sanguinipennis*	1
Eucnemidae			
	Isorhipis	*obliqua*	45
		Alternate	1
		BrownBlack	1
		FlatBlack	2
		GoldenHair	1
		LittleSquare	3
		Serrate	1
		SparseRound	1
		Tube BlackBack	18
		TwoLine	3
Histeridae			
	Teretrius	*Lollipop*	1
		Clown3.5	15
		Digger	3
Laemophloeidae			
	Charaphloeus	*TeaCup*	11
	Laemophloeus	*biguttatus*	1
	Laemophloeus	*megacephalus*	1
	Laemophloeus	*StrongLine*	1

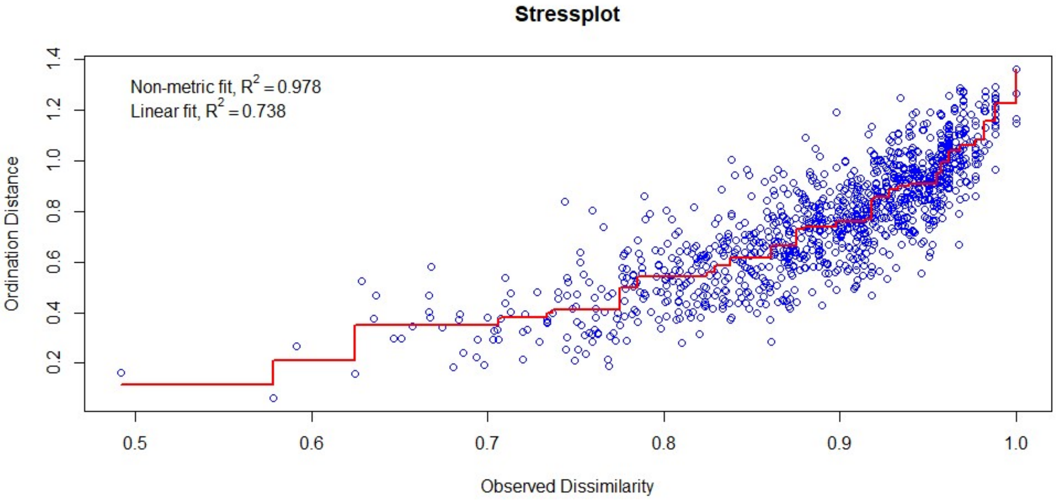
		Laemo One	16
Latridiidae			
	Corticaria	*ToothNeck*	1
	Melanophthalma	*Little Brown*	1105
	Melanophthalma	*Little DarkBrown*	1
	Stephostethus	*Hourglass*	5
Leiodidae			
	Leiodes	*Solo*	1
		Smashed	1
Lycidae			
	Calopteron	*terminale*	1
Melandryidae			
	Dircaea	*liturata*	3
Monotomidae			
	Bactridium	*ShinyLine*	6
	Europs	*pallipennis*	2
	Rhizophagus	*SquareNotum*	4
Mordellidae			
	Mordellaria	*serval*	13
	Mordellaria	*undulata*	6
	Mordellistena	*limbalis*	2
	Mordellistena	*NoPattern*	19
	Yakuhananomia	*bidentata*	2
		Batman	2
		Black	7
		FadeToBlack	128
		Heart	3
		JetFighter	17
		Monster	1
		OrangeBlackSpot	6
		OrangeShoulder	11
		Pale	8
		RedStripe	1
		SixStripe	1
		StripeBareLeg	8
		Tiger	4
		Triangle	3
		TwoTone	8
		VelvetSpots	1
		YellowShoulder BlackSpot	1
Mycetophagidae			
	Litargus	*BrownMottled*	15
	Litargus	*Shadow*	1
	Litargus	*tetraspilotus*	4
	Mycetophagus	*punctatus*	2
	Mycetophagus	*SandySpot*	1
	Mycetophagus	*serrulatus*	1
		Yellow	1
Nitidulidae			
	Amphicrossus	*ciliatus*	2

	Carpophilus	*antiquus*	7
	Carpophilus	*BlackBrownEdge*	13
	Carpophilus	*OldBrown*	11
	Colopterus	*semitectus*	3
	Colopterus	*unicolor*	1
	Epuraea	*BrownSmooth*	2
	Glischrochilus	*fasciatus*	27
	Glischrochilus	*quadrisignatus*	1
	Glischrochilus	*sanguinolentus*	13
	Omosita	*nearctica*	1
	Prometopia	*sexmaculata*	2
	Stelidota	*geminata*	15
		Light Brown	1
		FlatTan	1
Phalacridae			
	Olibrus	*RoundBrown*	5
	Stilbus	*Shiny*	2
Ptilodactylidae			
	Ptilodactyla	*BrownFade*	6
Ptinidae			
	Caenocara	*oculata*	1
	Trichodesma	*klagesi*	1
		Antlers	2
		FakeScarab	1
		GoldFur	1
		SnaggleTooth	1
Pyrochroidae			
	Dendroides	*canadensis*	1
	Neopyrochroa	*flabellata*	5
Scarabaeidae			
	Aphodius	*ShovelNose*	1
Silphidae			
	Nicrophorus	*orbicollis*	1
Silvanidae			
	Silvanus	*muticus*	15
Staphylinidae			
	Bisnius	*LongBBOO*	66
	Bisnius	*LongBOBO*	11
	Carphacis	*dimidiatus*	1
	Euconnus	*Euconnus One*	2
	Hesperus	*apicialis*	4
	Lordithon	*Lordithon Vague*	1
	Lordithon	*Dark*	1
	Palaminus	*SuperCool*	1
	Philonthus	*caeruleipennis*	5
	Pycnoglypta	*campbelli*	11
	Sepedophilus	*GoldComb*	3
	Sepedophilus	*Nice5mm*	1
	Sepedophilus	*SmallComb*	1
	Sepedophilus	*Sepedophilus*	1

	Siagonium	*americanum*	1
	Upoluna	*batrisioides*	1
		BHeadFur	6
		BNNN	11
		GemStone	1
		SmallLong	4
Synchroidae			
	Synchroa	*punctata*	1
Tenebrionidae			
	Anaedus	*brunneus*	1
	Meracantha	*contracta*	1
		CombClaw One	1
Tetratomidae			
	Hallomenus	*scapularis*	1
	Penthe	*pimelias*	1
Throscidae			
	Aulonothroscus	*pugnax*	2
Trogossitidae			
		Shovelnose	4
Zopheridae			
	Synchita	*parvula*	1

Appendix E: NMDS k selection and Stressplot





Appendix F: Summary Tables of Generalized Mixed Models

Abundance				
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	4.3490	0.1267	34.339	< 2e-16
Age Old	-0.1290	0.0456	-2.829	0.0047
Second Period	-0.0193	0.0418	-0.460	0.6452
Third Period	-0.6760	0.0507	-13.342	< 2e-16
CWD	-0.0599	0.0378	-1.585	0.1131
HS	-0.2703	0.0388	-6.974	3.08e-12
Age Old * HS	0.6020	0.0816	7.376	1.63e-13
CWD * HS	0.1807	0.0466	3.875	0.0001

Richness				
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	2.6078	0.1100	23.722	< 2e-16
Age Old	-0.0641	0.0838	-0.765	0.4445
Second Period	-0.2323	0.0902	-2.575	0.0100
Third Period	-0.5776	0.1100	-5.253	1.49e-07
CWD	0.0767	0.0423	1.812	0.0700
HS	-0.0976	0.0474	-2.059	0.0395
Abundance	0.0036	0.0010	3.772	0.0002

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