January 2011

Land snail species diversity and composition between different forest disturbance regimes in central and eastern Kentucky Forests

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Recommended Citation

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https://encompass.eku.edu/etd/32

LAND SNAIL SPECIES DIVERSITY AND COMPOSITION BETWEEN DIFFERENT DISTURBANCE REGIMES IN CENTRAL AND EASTERN KENTUCKY FORESTS

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Date 13 June 2011

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By

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Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
June, 2011

DEDICATION

This thesis is dedicated to my mother and father, Debbie and Davey Douglas, without whom none of this would have been possible. They taught me from a very young age that hard work and persistence were the keys to success. They have been beside me every step of the way and have always encouraged me to reach for my goals, never give up, and always do the best that I can. I am forever grateful for their unwavering love and support.

ACKNOWLEDGEMENTS

Without the support of many people and organizations, I would most likely still have my head buried in a soil sieve full of leaf litter picking through micro-snails. I would like to take this opportunity to thank everyone who has had a hand in shaping this project.

First and foremost, I would like to thank The Kentucky Society of Natural History, the Kentucky Academy of Science, and the Division of Natural Areas at Eastern Kentucky University for funding this research. Without the financial support of these organizations, seeing this study to completion would have been a difficult task.

I would like to acknowledge my major professor, Dr. David R. Brown, for his guidance, support, and help with data collection throughout this project as well as for teaching me the art of four square, a skill that will always come in handy no matter what the situation may be. I owe Dr. Neil Pederson a debt of gratitude for showing me that studying land snails is where I belong and for always encouraging me to never deviate very far from where my true passion lies. I would also like to thank Dr. David Hayes for allowing a terrestrial ecologist the use of an aquatic ecologist's lab space and equipment and for tolerating all my practical jokes. Dr. Stephen Richter was always there for me to talk to and offer needed advice on an array of topics and for that I am very thankful. Dr. Tyler Smith offered much needed assistance with ordination and multivariate statistical analyses and I am very thankful for his help as well.

I am extremely grateful to Dr. Ronald S. Caldwell and Daniel C. Dourson. These individuals first introduced me to land snails and the immense research possibilities that exist therein, and for that I am extremely appreciative. Ron, Dan, and Dr. John

Slapcinsky, of the Florida Museum of Natural History, helped substantially with identifications and checking my species lists during the course of this project as well.

I am also indebted to Dr. Melinda Wilder of EKU Natural Areas and Robert Watts, Superintendent at Lilley Cornett Woods, for allowing me access to the property there, giving me guidance, and orienting me to the property. Beverly James and Zeb Weese of the Kentucky State Nature Preserves Commission helped immensely with access to Floracliff and Blanton Forest State Nature Preserves. Brandon Howard of the Kentucky Division of Forestry helped a great deal with site location and orientation to different areas at Kentenia State Forest in Harlan County. I would also like to acknowledge Byron Brooks at the Kentucky State Nature Preserves Commission for fulfilling my numerous requests for Geographic Information Systems data regarding nature preserves properties. I am also indebted to Mark Gumbert and Copperhead Consulting for lending me equipment and allowing me to use lab space. I am also very grateful for the employment opportunities that they have given me over the past three years.

I greatly appreciate my friends Amy and Wayne Van Devender for suggesting that I attend their land snail identification workshop at Highlands Biological Station. That workshop helped, and still is, hone my identification skills. I would like to acknowledge my friend Michelle Guidugli for help in the field on some very hot June days at Floracliff State Nature Preserve. I would also like to thank my friend and office mate, Rob Denton, for advice, listening to me vent, and most importantly, comic relief. I’m fairly certain that without his friendship, my red beard would most definitely be gray right now.

Finally, I am forever grateful to my girlfriend, Andrea Drayer, for always being there for me in the field, lab, and at home. Without her constant companionship and love, I never would have made it through this project. I am very lucky to have someone such as her to always be there.

ABSTRACT

Land snails are cornerstone organisms that contribute to properly functioning ecosystems. However, habitat loss and destruction have led to these organisms being one of the most imperiled groups on the planet. Due to their relatively sedentary nature, land snails can be susceptible to anthropogenic disturbance and habitat fragmentation. Because of this, old-growth forests have the potential for being premiere habitat for these organisms, and snails have the potential to be good indicators of old-growth habitats. This study compared land snail species diversity and community composition in old-growth and second-growth forests in the Inner Bluegrass, Cumberland Plateau, and Pine Mountain ecoregions of Kentucky. Study areas were selected in central and eastern Kentucky based on disturbance histories. Within each study area, data regarding species diversity, richness, and abundance between disturbance classes was collected and analyzed using a random effects analysis of variance as well as non-metric multidimensional scaling to compare community structures. Habitat data was analyzed using canonical correspondence analysis. In the Inner Bluegrass Region, the snail diversity was high, and had low variability between sampling plots, but community composition differed significantly between the disturbance classes. In the Cumberland Plateau and Pine Mountains sites, species diversity and abundance was higher in the undisturbed forests compared to disturbed forests. There was also high variability in species composition among the sampling plots within these sites. Non-metric Multidimensional Scaling highlighted variation in community structure across all study sites. In the Inner Bluegrass, two distinct communities emerged with complete separation based on disturbance, whereas sites on the Cumberland Plateau and Pine

Mountain showed more overlap between disturbance regimes. Canonical correspondence analysis showed that relationships between land snails and environmental factors were variable across all study sites as well. Coarse woody debris, pH, soil moisture, aspect, duff accumulations, herbaceous cover and shrub height all had strong environmental relationships with the snail communities present, but differed in terms of what disturbance class they were correlated with across the study areas. Eighteen species were shown to be statistically significant indicators of undisturbed forests. However, these species were not found at all sites, so the utility of using these species as indicators across a broad geographical region may be limited. However, on an ecoregional scale, micro-snails showed more affinity for the undisturbed habitat than macro-snails. These findings highlight the complexity of snail communities across ecoregions and disturbance classes, as well as the potential utility of land snails as indicators of ecological conditions on regional levels. These results also reinforce evidence of the effects of anthropogenic disturbances on community composition. These findings support efforts to maintain ecological integrity by protecting areas with minimal historical human disturbance.

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CHAPTER I

INTRODUCTION

Disturbance-based stressors can change forest communities and alter normal ecosystem processes (Bormann and Likens 1979, Likens et al. 1996). Old-growth forests are among the best examples of unaltered communities and ecosystems, and can be used as the best-available reference of historic conditions for managers and biologists. Although the definition of old-growth forests has been debated heavily (Hunter 1989, Tyrell 1992, Leverett 1996, Hunter and White 1997, Frelich and Reich 2003, Wirth et al. 2009), these areas are often indicated by characteristics of forest structure, the landscape, and individual trees (Oliver and Larson 1996, Pederson 2010). In Kentucky, old-growth is generally designated by canopy trees that pre-date the settlement of Kentucky (ca. 1680) (Martin 1992).

The effects of disturbance in forests are manifested and easily observed at the level of the forest floor. The herbaceous layer of disturbed forests takes many decades (reports suggest 87 to >150 years) to recover to the species richness and abundances present in primary forests, and complete recovery may be inhibited by global change (Duffy and Meier 1992, Meier et al. 1995, Wyatt and Silman 2010). By altering the forest floor, anthropogenic disturbances may prevent plant communities, and their associated animal communities from returning to pre-disturbance levels (Bormann and Likens 1979, Seastedt and Crossley 1981). These community changes may cause additional adverse ecological effects including changes to decomposition and nutrient cycling of organic material on the forest floor (Coleman et al. 2004).

The effects of disturbance on amphibians that live on the forest floor are well documented. Clear cutting results in immediate drastic declines in terrestrial salamander (Plethodontidae) populations followed by their absence from these areas for several decades (Pough et al. 1987, Ash 1988, Dupuis et al. 1995, Ford et al. 2002). The effects of timber harvest on southern Appalachian salamander populations and their continued absence for decades thereafter suggest that it may take these populations 50-70 years to fully recover to pre-logging population levels (Petranka et al. 1993, Petranka et al. 1994, Bratton and Meier 1998, Ford et al. 2002, Semlitsch et al. 2009). This is primarily due to the opening of canopies which alters conditions near the ground. Local extinctions of salamanders may also be caused by the sequence of logging and fire, as well as from competition with other native salamanders for refugia (Pauley 2008). Conversely, natural disturbances typically are less severe and smaller scale than anthropogenic disturbances (Greenberg 2001).

The effects of disturbance on other groups of vertebrates are complex. Birds and reptiles, as well as amphibians, can show immediate negative impacts including population declines in response to forest management practices (Gram et al. 2003, Knapp et al. 2003, Renken et al. 2004). Edge effects created by roads have been shown to cause drastic decreases in salamander populations nearly 20 meters from these areas (Marsh and Beckman 2004). However, in areas like parks and preserves, where walking and hiking trails are an important component of the landscape, coarse woody debris may be cleared from these trails, cut into small manageable pieces and discarded just off trial creating good wildlife habitat that might not be present otherwise (Davis 2007).

Natural disturbances may also cause seemingly contrasting effects. Disturbances such as hurricanes along coastal areas play key roles in structuring breeding bird communities in that they alter both canopy and understory vegetation, resulting in decreased densities for some species, and increased densities of others (Brown et al. 2011). In contrast, small scale natural disturbances, such as windfall canopy gaps, have little effect on terrestrial salamander populations, probably because the effects occur at a small scale (Greenberg 2001).

In soil invertebrates, such as earthworms, low levels of disturbance do not appear to have significant effects on diversity and composition (Kalisz and Powell 2000). In contrast, soil disturbance and forest fragmentation alter communities, and lead to colonization of invasive species (Kalisz and Dotson 1989). Again, edge effects created by roads have been shown to drastically effect macroinvertebrate populations up to 100 m away from these areas (Haskell 2000), much as it does with amphibians. Thus, disturbance can be both beneficial and detrimental depending on severity and species natural history.

Land snails (including slugs), along with micro-arthropods, are crucial parts of a properly functioning ecosystem (Caldwell 1993, Coleman et al. 2004). These organisms are important in nutrient cycling (Burch and Pearce 1990), and are among some of the most imperiled species on the planet (Lydeard et al. 2004). Snails can also have important ecological effects on terrestrial vertebrates (Harper and Guynn 1999). As a food source, snails can be a vital source of calcium for birds and small mammals (Graveland et al. 1994, Graveland and van der Wal 1996, Hames et al. 2002, Allen 2004). Through ingestion and defecation, land snails may serve as potential agents of dispersal for fungi, some of which are beneficial to the root systems of forest vegetation, and aid in decomposition of coarse woody debris (Caldwell 1993, Keller and Snell 2002). Snails may also play a role in detoxification of forest soils. As empty shells of dead mollusks decompose, toxic materials sequestered within those shells breakdown at a rate that allows consumers to metabolize these materials (Pearce 2008).

Land snails may be useful indicators of ecosystem health and habitat quality. Because of their critical ecosystem services, declines in land snail communities may indicate broader problems with the health of the ecosystem. For instance, acid precipitation and timber harvest greatly reduce calcium levels in the soil (McLaughlin and Wimmer 1999) and lead to declining snail populations, such declines may forewarn of other ecological effects (Wareborn 1992, Hotopp 2002). Additionally, the limited mobility of land snails makes the presence of some species potential indicators of high quality, undisturbed habitats (Shimek 1930, Cameron and Williamson 1977, Watters et al. 2005). Mark recapture studies have found that movements of relocated *Cepea nemoralis* Linnaeus, 1758, a land snail measuring 25 mm in diameter, averaged 2.0 m at four weeks, 3.4 m at fourteen weeks, and 5.5 m after one year indicating particularly small home ranges (Goodhart 1962). Other research of land snail movements showed that gastropods similar in sizes to those studied here can move on average of 76 – 225 cm per day (McCracken 1976, Auffenberg and Auffenberg 1988, Pearce 1990). A much larger species, *Achatina fulica* (Ferrusac, 1821), (~ 60 mm in diameter), can move up to 500 m over a six month period (Tomiyama and Nakane 1993). There has been limited research on movements of micro-snails (< 5 mm in diameter). One species of micro-snail, *Punctum pygmaeum* (Draparnaud, 1801), moved an average distance of only 47 mm over a 12 hour period in a laboratory setting (Baur and Baur 1988). It is likely that other micro-snails have similarly limited movements. Passive dispersal can occur by attaching to the feathers and feet of birds (Huey 1936) and by human activities, such as attaching themselves to vehicles and being transported to new areas and by attaching themselves to nursery stock, but in general the importance of these mechanisms is poorly understood (Aubry et al. 2006).

Land snails are highly dependent on microhabitat conditions (Boycott 1934, Burch 1955, Beyer and Saari 1977), including the presence of coarse woody debris (CWD). Up to 25 percent of the land snail fauna of the southeastern United States rely on CWD (Caldwell 1993), and this dependence appears to hold throughout the world (Kappes 2005). CWD accumulations tend to be higher in areas with relatively low intensity of anthropogenic disturbance (Webster and Jenkins 2005). For example, in areas that were not salvage-logged following the Chestnut Blight, large accumulations of dead and fallen Chestnuts (*Castanea dentata* Marsh.) persist (Muller and Liu 1991), creating abundant suitable land snail habitat. Natural disturbances in old-growth forest can cause decadal variation in CWD abundance (Muller 2003), creating a spatially and temporally dynamic pattern of habitat quality for land snails.

Landscape position factors such as slope and aspect can indirectly control the presence of land snails (Coney et al. 1982, Petranka 1982, Dourson and Beverly 2008). Land snails are most diverse and abundant in areas of high leaf litter moisture and a thick organic soil horizon (Nekola 2003). This moisture is needed for basic physiological processes including locomotion and egg survival (Burch and Pearce 1990).

Lower densities of land snails have been found in early-successional forests compared to old-growth forests, and this pattern was correlated with soil moisture (Shikov 1984). Watters (2005) did not find significant differences in snail species richness between reclaimed strip mines and relatively undisturbed habitat in Ohio; however, many of the species found in strip-mined areas belonged to families that Shikov (1984) identified as being well adapted to disturbance. Watters also collected several non-native species in the disturbed areas suggesting that disturbance may create corridors for the movement and establishment of invasive snails.

Land snail community composition may be driven by the frequency of fire, with frequent fires locally eliminating some species (Severns 2005). Re-colonization of burned areas may occur from external populations as well as from small refugia present within the burned areas, however, intense fires may severely impact these refuges and reduce the probability of re-colonization from within the area (Kiss and Magnin 2003). Regardless of the source population, the composition of the colonizing land snail communities will depend heavily on the habitat structure, topography, and floristic composition of the forest that succeeds the disturbance (Kiss and Magnin 2003).

The primary objective of this study was to determine if differences in land snail communities exist between different anthropogenic forest disturbance regimes present in central and eastern Kentucky. The main anthropogenic disturbance in the forests in this study was logging, however, some areas studied have experienced small scale, infrequent forest fires, small scale agricultural practices, and contain areas that were cleared for human inhabitance. I hypothesized that snail communities would differ between old-growth and second-growth forests, and differences would be correlated with environmental factors. Specifically, I predicted that because land snails are specialized and dependent on specific microhabitats, areas having past histories of severe anthropogenic disturbances would support fewer species in lower numbers than areas that have experienced lower levels of disturbance. Furthermore, because life history traits such as tolerance to desiccation, dependence on CWD, and other habitat characteristics related to disturbance vary among species, another goal of this research was to examine whether individual species could be used as indicators of forest disturbance, or conversely, as indicators of old-growth conditions.

CHAPTER II

STUDY AREAS

Inner Bluegrass Ecoregion: Floracliff State Nature Preserve

Floracliff State Nature Preserve is located in Fayette County, Kentucky (Figure F1, APPENDIX F) approximately 24 km south of the city of Lexington. The 116 ha preserve is located along the Kentucky River Palisades adjacent to Interstate 75 and is bisected by Elk Lick Creek (Floracliff 2011a).

Floracliff is located in the Inner Bluegrass physiographic region of Kentucky (Figure F2) (Fenneman 1938). This region is noted for having rich and fertile soils. Specifically, Floracliff is located in the Interior Plateaus ecoregion (Level III) (Figure F3) (EPA 2002), and Inner Bluegrass ecoregion (Level IV) of Kentucky (Figure F4) (Woods et al. 2002). Geologically, the inner bluegrass area is underlain by Lexington and Cynthiana limestone, of the Ordovician geologic time period (McFarlan 1943).

Floracliff lies in a transition zone from mixed mesophytic forests to the east and oak-hickory forests to the west (Braun 1950). Species present represent vegetation elements of both of these areas as well as some non-native species (Table A1, APPENDIX A). The property where the preserve sits today has changed ownership several times over the last 225 years. The vast majority of the Kentucky River palisades area was logged around the turn of the 20th century and later used primarily for agricultural practices (Floracliff 2011b). However, despite having experienced these anthropogenic disturbances, there are two distinct areas present at Floracliff that contain trees that are hundreds of years old (Figure F5). The first of these stands contains trees that are greater than 200 years of age, in fact, the oldest known tree in the state, a 400 year old *Quercus muehlenbergii* Eng., is located here. The other stand contains trees that are less than 125 years of age.

Cumberland Plateau ecoregion: Poll Branch and Lilley Cornett Woods

Poll Branch and Lilley Cornett Woods are located near the community of Skyline in Letcher County in the southeastern portion of Kentucky (Figure F1). Poll Branch is approximately 89 hectares in size and is located just outside the boundaries of Lilley Cornett Woods and parallels Big Everidge Hollow (Figure F6). Poll Branch is second-growth forest comprised of mixed mesophytic communities (Muller and Martin 1983) Lilley Cornett Woods Appalachian Ecological Research Station contains both second-growth and old-growth forests (224 ha total with 102 ha of old-growth) (Figure F7). Within Lilley Cornett, I sampled the 52 ha Big Everidge Hollow, which is old-growth forest (Martin 1975).

These sites are located within the Appalachian Plateaus physiographic province (Figure F2) (Fenneman 1938), in the Central Appalachian ecoregion (Level III) (Figure F3) (EPA 2002), and Dissected Appalachian Plateau (Level IV) ecoregion of Kentucky (Figure F4) (Woods et al. 2002). The area is maturely dissected plateaus that are underlain by sandstones, shale, siltstones and coal of the Breathitt formation, from the middle and lower Pennsylvanian age (McFarlan 1943, Puffett 1965, Martin 1975).

The forests of Poll Branch and Big Everidge Hollow are principal examples of the mixed mesophytic forest type (Braun 1950, Martin and Shepard 1973, Muller and Martin 1983) and have high species richness (Table A1). Nine overstory communities have been recognized and mapped at Lilley Cornett Woods and are as follows: Beech, Beech-buckeye, Beech-sugar maple, Beech-white oak, Chestnut oak, Mixed oak, White oak, Hemlock, and Sugar maple-basswood-tulip poplar (Martin 1975).

Lilley Cornett Woods has been managed by Eastern Kentucky University's Division of Natural Areas since 1969. Since that time, the area has only experienced one major anthropogenic disturbance, a low intensity fire that burned approximately 28 hectares in Big Everidge Hollow in the spring of 2010 (pers. observ.-9 June 2010). Otherwise, the area has been free of agriculture activities, logging, or any other fire events since 1969 (Galbraith and Martin 2005). Prior to that, the area was grazed by domestic livestock until the 1950s and evidence of fire events in the early 20th century are confined to older trees (Galbraith and Martin 2005) and only evident by dendrochronology (Pederson pers. comm.).

Poll Branch has experienced more numerous severe anthropogenic disturbances than Lilley Cornett Woods. The area regenerated naturally following a clear-cut in 1945 (Muller and Martin 1983), and was contour-coal-mined in 1970 between 410 and 470 m in elevation (Muller 1982). Other disturbances include a road constructed to haul coal and a drained impoundment along the stream that flows through the hollow (pers. observ.-8 July 2010).

Pine Mountain ecoregion: Kentenia State Forest and Blanton Forest State Nature Preserve

Kentenia State Forest and Blanton Forest State Nature Preserve are located in Harlan County in the southeastern portion of Kentucky (Figure F1) approximately 24km northeast and 9 km west, respectively, of the city of Harlan. The two forests are 8 kilometers apart on the southeastern slope of Pine Mountain (Figure F8 and F9). Blanton

Forest encompasses 1264 ha of both old-growth and second-growth forests making it the largest tract of old-growth forest in the state of Kentucky (Napier 2010). Kentenia State Forest encompasses 1652 ha of second-growth forests. Both sites are very diverse ecosystems with forest communities ranging from mountain top acid seeps (bogs) to mixed mesophytic deciduous forests (Napier 2010).

Pine Mountain lies in what is often referred to as the Eastern Coalfields, which are also known as the Appalachian Plateaus physiographic region (Figure F2). Fenneman (1938) considered Pine Mountain to be part of the Cumberland Mountains section of the Appalachian Plateaus province. Pine Mountain is located within the Central Appalachians ecoregion (Level III) (Figure F3) (EPA 2002), and Cumberland Mountain Thrust Block (Level IV) ecoregion of Kentucky (Figure F4) (Woods et al. 2002). The southeast face of Pine Mountain is composed of sandstones primarily from the Lee Conglomerate and all formations are mainly from the Lower Pennsylvanian geologic time period (McFarlan 1943).

The Pine Mountain study areas are diverse, but dominated by Hemlock and Oak species (Table A1) (Braun 1950, McIntosh 2009, Napier 2010). Aside from small fire events, the old-growth portions of Blanton Forest have not experienced any major anthropogenic disturbances. Several trees found at this site have been dated to the late 1600's (Napier 2010). Kentenia State Forest has experienced major logging events over the last century as well as small scale fire events (McIntosh 2009).

CHAPTER III

METHODS

I sampled land snails in two sites in each of three ecoregions in eastern and central Kentucky. The ecoregions sampled were the Inner Bluegrass, Cumberland Plateau (Dissected Appalachian Plateau), and Pine Mountain (Cumberland Mountain Thrust Block) (Figure F4). Sites were selected based on disturbance history. In the Inner Bluegrass, two stands with different tree ages were paired (one with trees < 125 years old and the other with trees > 200 years old). Cumberland Plateau and Pine Mountain sites had paired areas of old-growth and second-growth forests. At each site, I sampled at 10 points (Total N = 60 points). The exact area of sampling differed among the points, but was approximately 100 m^2. All sampling occurred over two summer seasons from May 2009 – September 2010. Points were opportunistically selected based on walk-through surveys of the area and professional knowledge of land snail habitat. Thus, the sampling approach was designed to maximize estimates of land snail abundance and species richness at each site. At each point, I collected data on snail communities using searches and leaf litter samples. I also measured abiotic and biotic variables at each point.

At each point, three 17 cm x 32 cm cloth bags were filled with leaf litter and detritus and brought back to the lab to search for micro-snails (< 5 mm in diameter). Litter was haphazardly grabbed from several locations within the search area. Litter bags were dried for approximately one month and then sorted using #4, 10, 16, and 35 soil sieves that were 30.5 cm in diameter (Coney et al. 1981). Live and empty shells of macro-snails (> 5 mm in diameter) were collected using hand raking and walk through surveys of 20 person minutes per point. After collection, live snails were euthanized by immersion in water for 24 hours. Specimens were then placed in 95% ethyl alcohol for 24 hours to kill bacteria and body tissue was removed from the shell. All shells were identified to species based on shell morphology. A dissecting microscope was used in the identification of all specimens collected.

Taxonomic keys developed by Pilsbry (1940, 1946, 1948), Burch (1962), Dourson (2006, 2011), Caldwell and Dourson (2008), Branson (1973), Emberton (1988, 1991), Nekola and Coles (2010), Thomas et al. (2010), and Slapcinsky and Coles (2004) were used to identify all specimens collected. Additionally, expertise on identification was sought from Ronald S. Caldwell at the Cumberland Mountain Research Center – Lincoln Memorial University, Daniel C. Dourson at the Belize Foundation for Environmental Education, and John Slapcinsky at the Florida Museum of Natural History. County records as well as range extensions were determined using Hubricht (1985), Branson (1973), Dourson (2008) and through the use of the databases available at the Field Museum of Chicago (Gerber 2008) and the Florida Museum of Natural History (FLMNH 2011). New records are reported in Table C1, APPENDIX C. Taxonomy was based on Turgeon et al. (1998) and Perez et al. (2008).

At each point, I established a 20 m x 20 m plot for collecting visual percent cover estimates of canopy, bare ground, leaf litter, rock, and coarse woody debris (CWD). Within each plot I also measured soil pH, soil moisture, duff depth, soil temperature, aspect, and slope. Duff depth was measured as the depth of the organic soil horizon. Soil temperature was taken using an Oakton Thermistor thermometer. Soil moisture and pH were taken using a Kelway soil tester. Descriptive box plots for each of these habitat variables are located in APPENDIX G.

Within each 20 m x 20 m plot, I nested a 4 m x 4 m plot to measure vegetation structure by visual estimation of percent density of shrubs 0-1 m and 1-3 m height categories, grasses, and herbaceous species (Capleanor 1968). At the center of this plot, I used a concave spherical densiometer to estimate curved linear canopy cover (Lemmons 1956). Basal area was estimated with a Cruz-All with a basal area factor (BAF) of 10. For every tree that fell in the BAF 10 I used a diameter tape to measure diameter at breast height (DBH). Tree species were recorded and basal area was calculated. Basal areas ± standard errors are reported in APPENDIX A.

Statistical Analyses

I conducted rarefaction analysis on each site using Program EstimateS (Colwell 2009). For each study plot, I calculated Shannon-Weiner diversity ($\log_e$), Shannon-Weiner evenness, and abundance using the Ecological Methodology software program (Krebs and Kenney 2009). I also used Ecological Methodology software to calculate community similarity between forest disturbance classes. I tested for differences in diversity, abundance, richness and evenness between forest disturbance classes using a random-effects factorial analysis of variance (ANOVA) in SPSS version 18. Because the error terms were normal and homogeneous among groups, an identity-link was used. I used a Tukey's post-hoc test to compare each ecoregion by disturbance regime.

I analyzed species composition using non-metric multidimensional scaling (NMS) (Kruskal 1964). The NMS analysis was conducted with PC-ORD 5.10 (McCune and Mefford 2006), and the figures were created using PAST 2.08 (Hammer et al. 2001). This type of ordination is an iterative approach to finding the best position of *n* objects in *k* dimensions. NMS is appropriate for sparse species matrices (i.e. cells with large numbers of zeroes), because it uses rank-distances and thus avoids assumptions of linearity (Clarke 1993, McCune and Grace 2002). I used Bray-Curtis dissimilarity to construct the distance matrix with 250 iterations. The number of axes was selected based on permutation analysis that compared stress values of actual runs of data with runs of randomized data. I conducted this analysis separately on each ecoregion, and using all ecoregions combined.

To test for differences in species composition between second-growth and old-growth, I conducted a Multiple Response Permutation Procedure (MRPP) (Zimmerman et al. 1985) with a Bray-Curtis dissimilarity measure using PC Ord 5.10 separately on each ecoregion and using all ecoregions combined. MRPP is a nonparametric procedure for testing the null hypothesis of no significant differences between two or more groups. It is used to detect differences in species concentrations between *a priori* groups.

I conducted Indicator Species Analysis (Dufrêne and Legendre 1997) for each disturbance class using PC Ord 5.10. I conducted this analysis separately on each ecoregion, and using all ecoregions combined. This type of analysis is useful in detecting and describing species that may be useful for indicating environmental conditions. This analysis combines relative abundance and relative frequencies to estimate concentrations of species abundances and the reliability of occurrence of species to defined classes. Indicator values (IV) range from zero (no indication) to 100 (perfect indication). Perfect indication occurs when a species is exclusively found in one class, in this case, a forest disturbance class. I used a Monte Carlo test with 4,999 randomizations, to test for statistical significance of each species as an indicator.

To assess habitat associations of land snails, I used Canonical Correspondence Analysis (CCA) (ter Braak 1986). The CCA analysis was conducted with PC-ORD 5.10, and the figures were created using PAST 2.08. I scaled the axes to visually optimize representation of sites. A Monte Carlo permutations test with 999 iterations was used to test the null hypothesis that there was no relationship between species and habitat matrices. All scores reported are weighted averages (WA). This analysis was conducted on each ecoregion separately.

CHAPTER IV

RESULTS

Snail sampling yielded 3196 individual snails, representing 15 families, 35 genera, and 70 species (Table 1). Species found at each study site are reported in Table B1, APPENDIX B. Fifty-five new county records were found and reported from Fayette, Letcher and Harlan counties highlighting that land snails currently are understudied in the literature (APPENDIX C). One species listed as endangered by the Kentucky State Nature Preserves Commission was found at Lilley Cornett Woods.(KSNPC 2010).

Table 1. Species of land snail collected at 3 study areas during 2009 and 2010. Species listed by the Kentucky State Nature Preserves Commission as endangered are shaded in gray.

Species	**# Collected**
CARYCHIIDAE	
Carychium clappi Hubricht, 1959	364
Carychium exile I. Lea, 1842	401
Carychium nannodes G.H. Clapp, 1905	332
COCHILICOPIDAE	
Cochilicopa moreseana (Doherty, 1878)	72
DISCIDAE	
Anguispira alternata (Say, 1816)	34
Anguispira kochi (Pfeiffer, 1821)	54
Anguispira mordax (Shuttleworth, 1852)	7
Discus patulus (Deshayes, 1830)	76
HAPLOTREMATIDAE	
Haplotrema concavum (Say, 1821)	64
HELICARNIDAE	
Euconulus fulvus (Muller, 1774)	22
Guppya sterkii (Dall, 1888)	51
HELICODISCIDAE	
Helicodiscus notius Hubricht, 1962	21
PHILOMYCIDAE	
Palifera dorsalis (A. Binney, 1885)	1
Philomycus carolinensis (Bosc, 1802)	2
POLYGYRIDAE	

Table 1. (Continued)

Species	**# Collected**
Appalachina sayana (Pilsbry, 1906)	59
Euchemotrema fraternum (Say, 1824)	47
Inflectarius inflectus (Say, 1821)	25
Inflectarius rugeli (Shuttleworth, 1852)	29
Mesodon elevatus (Say, 1821)	26
Mesodon normalis (Pilsbry, 1900)	18
Mesodon thyroidus (Say, 1816)	20
Mesodon zaleatus (A. Binney, 1837)	18
Patera appressa (Say, 1821)	38
Stenotrema angellum Hubricht, 1958	16
Stenotrema barbatum (G.H. Clapp, 1904)	14
Stenotrema stenotrema (Pfeiffer, 1842)	25
Neohelix albolarbis (Say, 1816)	20
Tridopsis sp.	3
Triodopsis tridentata (Say, 1816)	59
Xolotrema denotatum (Ferussac, 1821)	21
POMATIOPSIDAE	
Pomatiopsis lipadaria (Say, 1817)	17
PUNCTIDAE	
Punctum minutissimum (I. Lea, 1841)	41
Punctum blandianum (Pilsbry, 1900)	12
PUPILLIDAE	
Columella simplex (Gould, 1841)	68
Gastrocopta armifera (Say, 1821)	75
Gastrocopta contracta (Say, 1822)	93
Gastrocopta contricaria (Say, 1816)	1
Gastrocopta pentodon (Say, 1821)	39
Gastrocopta procera (Gould, 1840)	71
Pupoides albilabris (C.B. Adams, 1841)	11
Vertigo bollesiana (E.S. Morse, 1875)	9
Vetigo gouldii (A. Binney, 1843)	9
Vertigo parvula Sterki, 1890	19
Vertigo tridentata Wolf, 1870	32
STROBILSOPSIDAE	
Stobilops aenea Pilsbry, 1926	20
Strobilops labyrinthica (Say, 1817)	15
SUCCINEIDAE	
Catinella oklahomarum (Webb, 1953)	18
VALLONIADAE	
Vallonia excentrica Sterki, 1893	12

Table 1. (Continued)

Species	# Collected
ZONITIDAE	
Gastrodonta interna (Say, 1822)	89
Glyphyalinia cryptomphala (G.H. Clapp, 1915)	13
Glyphyalinia indentata (Say, 1823)	64
Glyphyalinia wheatleyi (Bland, 1883)	91
Hawaii miniscula (A. Binney, 1840)	62
Mesomphix cupreus (Rafinesaue, 1831)	18
Mesomphix inornatus (Say, 1821)	67
Mesomphix perlaevis (Pilsbry, 1900)	30
Paravitrea capsella (Gould, 1851)	33
Paravitrea placentula (Shuttleworth, 1852)	3
Striatura meridionalis (Pilsbry and Ferriss, 1906)	34
Striatura ferrea E.S. Morse, 1864	14
Ventridens demissus (A. Binney, 1843)	26
Ventridens gularis (Say, 1822)	62
Ventridens intertextus (A. Binney, 1841)	15
Ventridens lasmodon (Phillips, 1841)	18
Ventridens lawae (W.G. Binney, 1892)	1
Ventridens ligera (Say, 1821)	29
Ventridens theloides (Walker and Pilsbry, 1902)	2
Zonitoides arboreus (Say, 1816)	22
Zonitoides elliotti (Redfield, 1856)	2
TOTAL	3196

Rarefaction analysis showed variation in species richness among sites, with apparent separation between disturbance classes (Figure 1). Second-growth sites had consistently lower species diversity compared to paired old-growth sites within the same region. Species richness at both Inner Bluegrass sites plateaued after just a few samples, suggesting that the sampling at these sites adequately represents the community, at least in terms of species richness (Figure H1, APPENDIX H). However, the other sites continued to add new species after 10 samples per site. Another noteworthy result is the high number of species found at the old-growth Cumberland Plateau site (Lilley Cornett Woods) compared to the second-growth site (Poll Branch) in the same area (Figure H2).

These two sites were similar in most abiotic and vegetation characteristics, but had different disturbance histories (Figure I1, APPENDIX I). Species richness at the two Pine Mountain disturbance regimes was similar after several samples; however, species richness between the sites separated with increased sampling (Figure H3). When combining all ecoregions, old-growth and second-growth sites had relatively high community similarities according to multiple indices (Table 2).

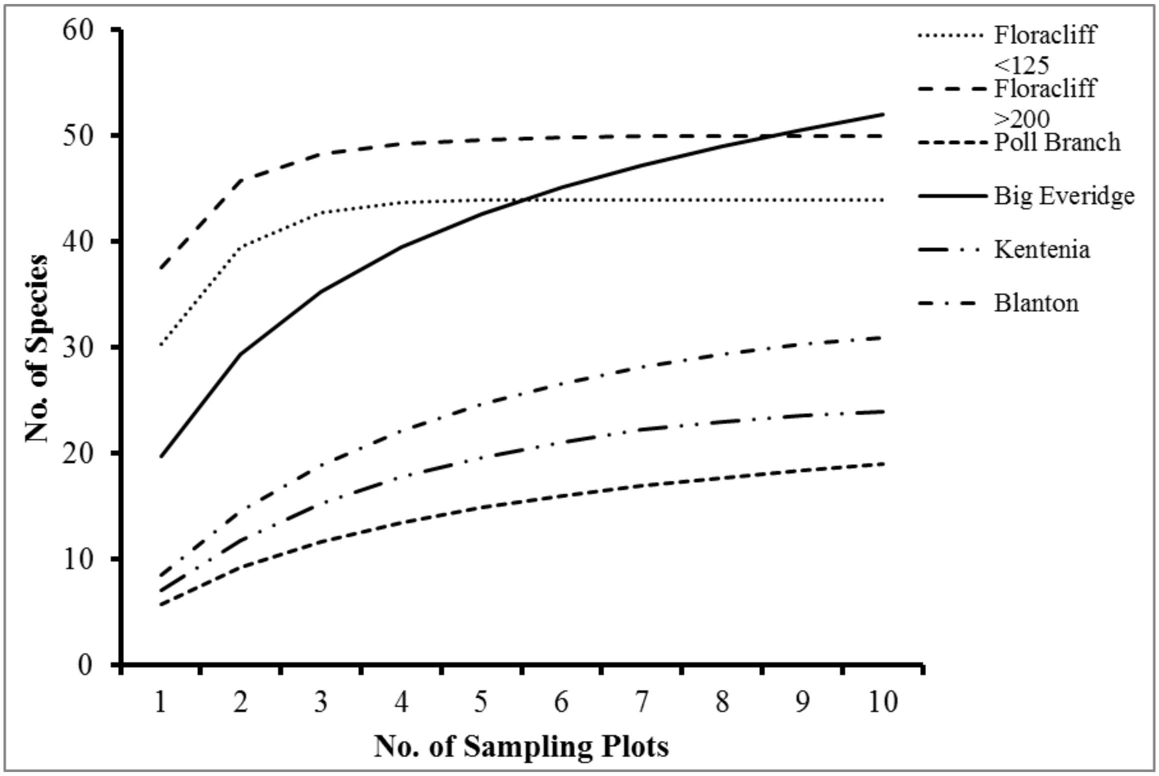

Figure 1. Rarefaction curves of the 6 study sites showing the rate of species accumulation across the sampling points.

Table 2. Similarity coefficients for second-growth vs. old-growth sites.

Similarity Index	Coefficient
Bray-Curtis	0.61
Euclidean	35.37
Horn	0.90
Morisita	0.93
Percent Similarity	74.34

Species diversity (Shannon-Weiner) was higher in each of the old-growth study sites compared to second-growth sites in the Inner Bluegrass and Cumberland Plateau ecoregions (Figure 2) (ANOVA: disturbance*region: $F_{2, 54} = 9.29$, $p < 0.001$; Inner Bluegrass: $q_{54} = 4.70$, $p < 0.001$; Cumberland Plateau: $q_{54} = 6.96$, $p < 0.001$). However, the Pine Mountain old-growth site did not differ in diversity compared to its paired second-growth site ($q_{54} = 0.939$, $p = 0.939$).

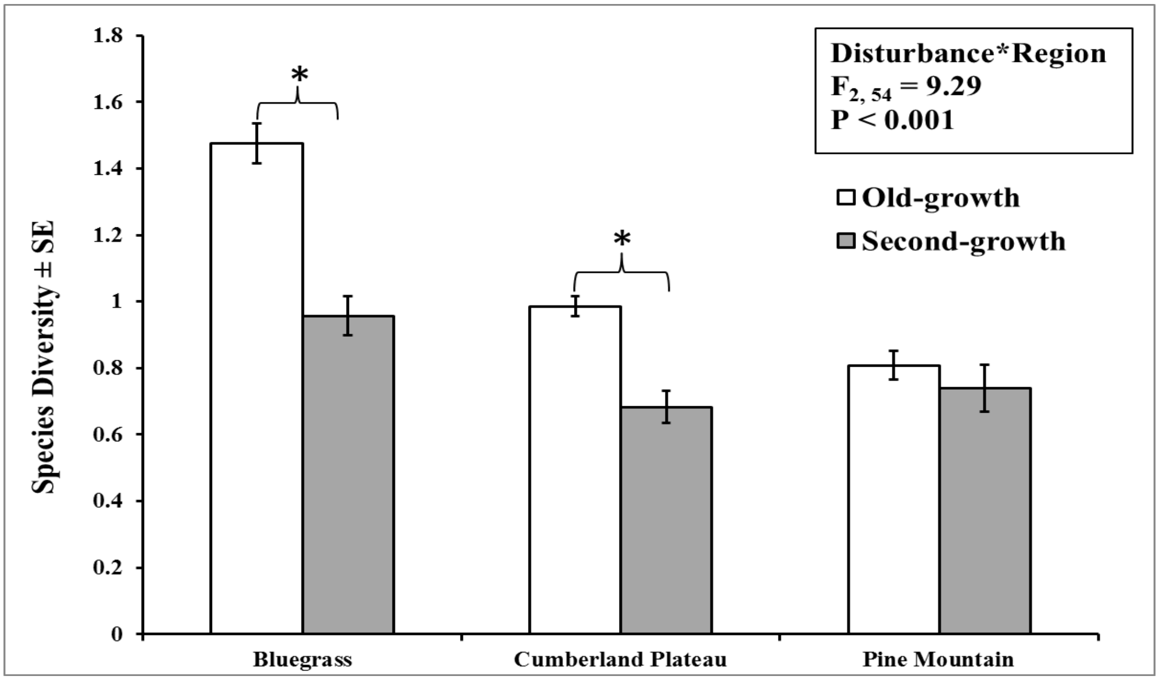

Figure 2. Mean Shannon-Weiner species diversity ± SE between paired old-growth and second-growth sites.

Species richness was higher in each of the old-growth sites compared to second-growth sites in the Inner Bluegrass and Cumberland Plateau ecoregions (Figure 3) (ANOVA: disturbance*region $F_{2,54} = 6.56$, $p = 0.003$; Inner Bluegrass: $q_{54} = 5.73$, $p < 0.001$; Cumberland Plateau: $q_{54} = 2.23$, $p < 0.02$) . However, the Pine Mountain old-growth site did not differ in richness compared to its paired second-growth site (q_{54} = 0.74, p = 0.97).

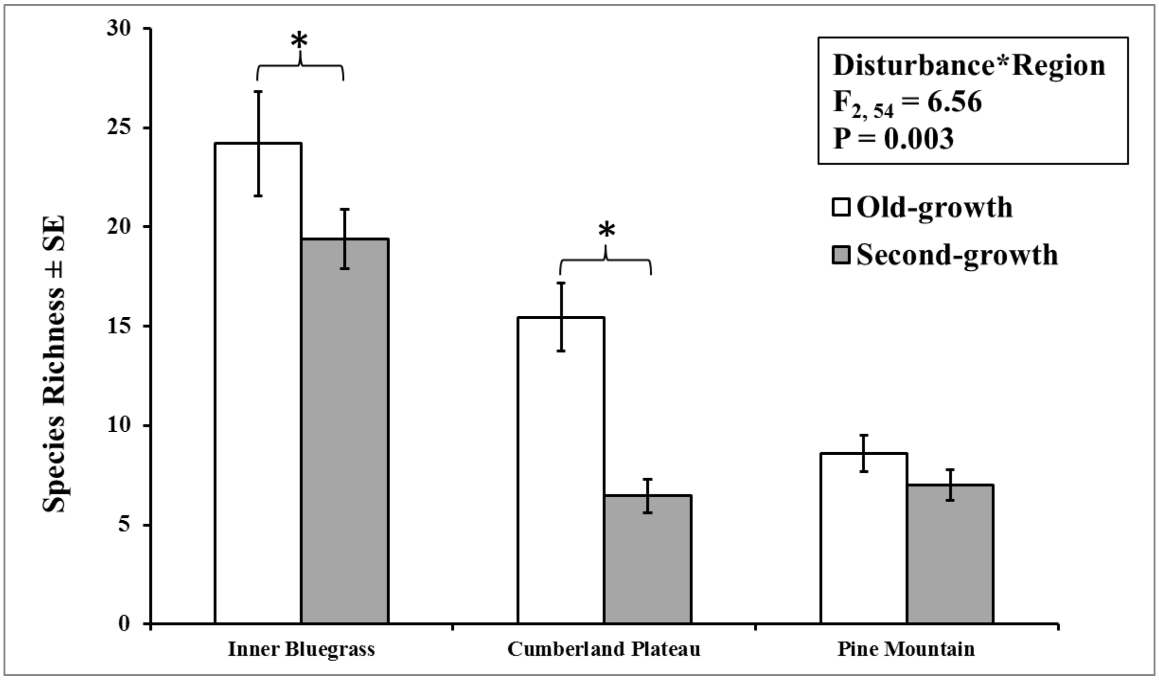

Figure 3. Mean snail species richness between paired old-growth and second-growth sites.

Abundance was higher in each of the old-growth study sites compared to second-growth sites in the Inner Bluegrass and Cumberland Plateau ecoregions (Figure 4) (ANOVA: disturbance*region $F_{2.54}$ = 9.50, p < 0.001; Inner Bluegrass: q_{54} = 5.49, p< 0.001; Cumberland Plateau: q_{54} = 5.67,p < 0.001). However, the Pine Mountain old-growth site did not differ in abundance compared to its paired second-growth site (q_{54} = 0.24, p = 1.00).

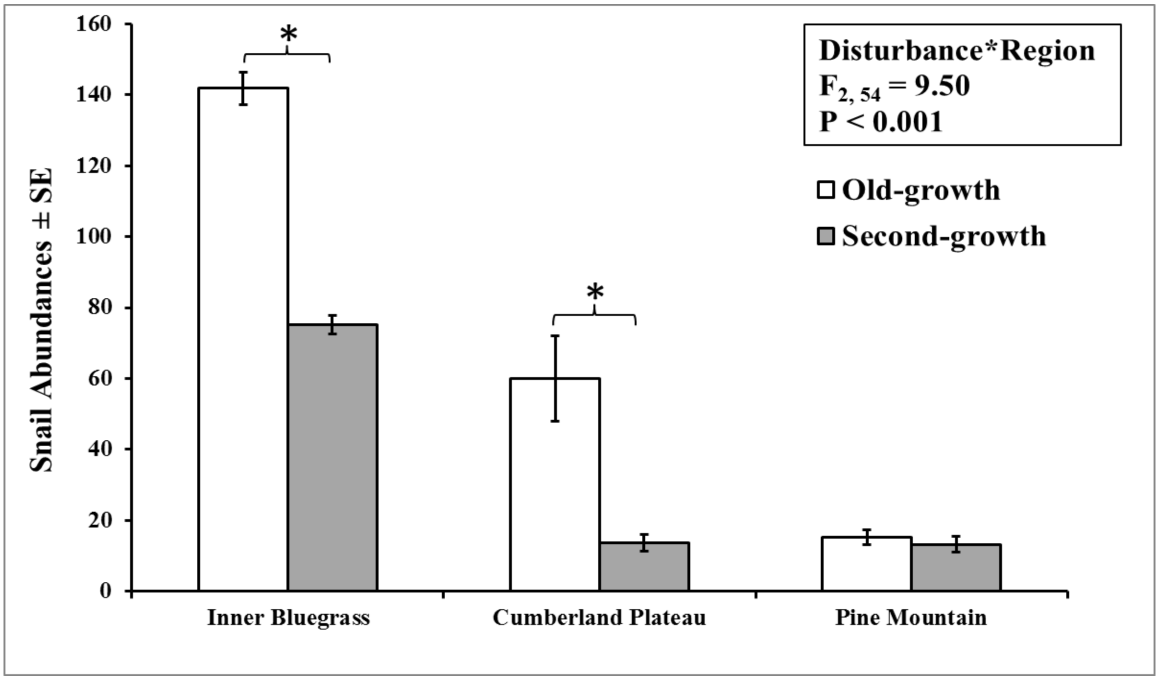

Figure 4. Mean snail abundances between paired old-growth and second-growth sites.

Shannon evenness values were similar across all ecoregions between the paired old-growth and second-growth sites (Figure 5) (ANOVA: disturbance*region $F_{2,54}$ = 0.674, p = 0.51; Inner Bluegrass: q_{54}= 1.30, p = 0.78; Cumberland Plateau: q_{54} = 0.07, p = 1.00; Pine Mountain: q_{54} = 2.18, p = 1.00). This indicates that the species collected were evenly distributed throughout both disturbance classes within each of the ecoregions sampled.

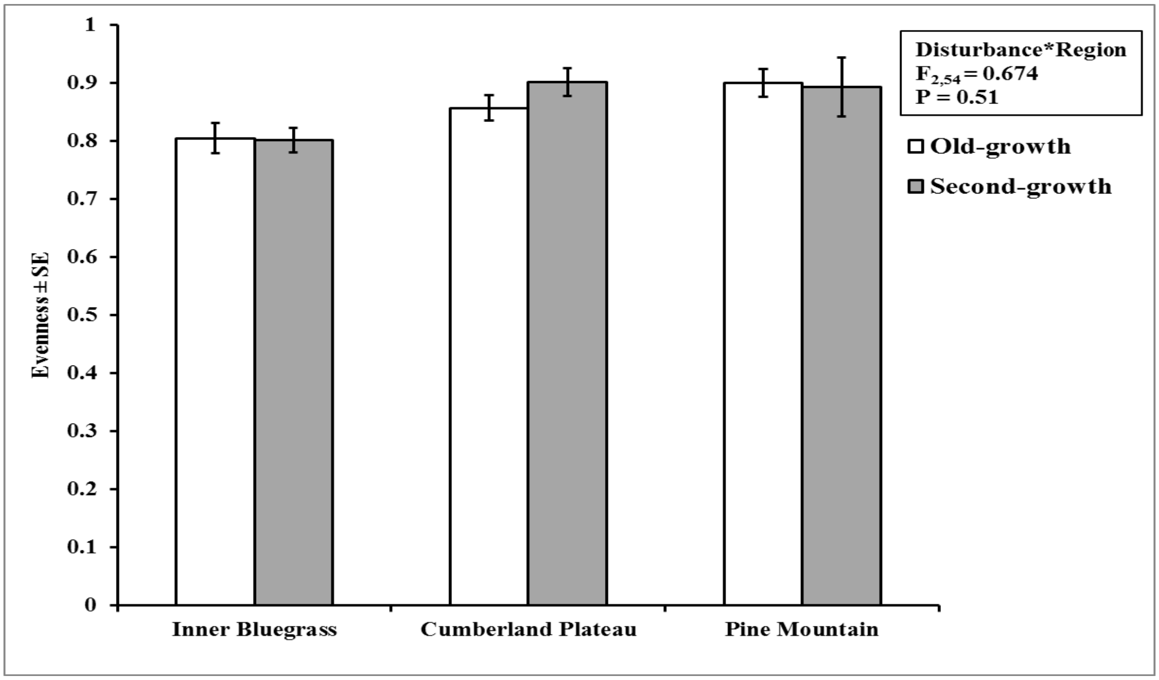

Figure 5. Evenness of snail species between paired old-growth and second-growth sites.

The NMS ordination across 60 sites indicated strong differences in species composition across the three regions to demonstrate the distinctiveness of assemblages among the physiographic and ecological regions in central and eastern Kentucky (stress = 21.56) (Figure 6). The degree of separation of snail communities between disturbance regimes varies among the regions. For instance, in the Inner Bluegrass, the separation between old-growth and second-growth is quite clear (Figure I1, APPENDIX I). In contrast, there appears to be greater overlap between old-growth and second-growth in both the Cumberland Plateau (Figure I2) and Pine Mountain (Figure I3) sites. However, it should be noted that some separation is evident in the Cumberland Plateau and Pine Mountain sites. Another interesting aspect of this ordination is that one region, the Inner Bluegrass (i.e., Floracliff), showed much less variation among sites and habitats than the other regions.

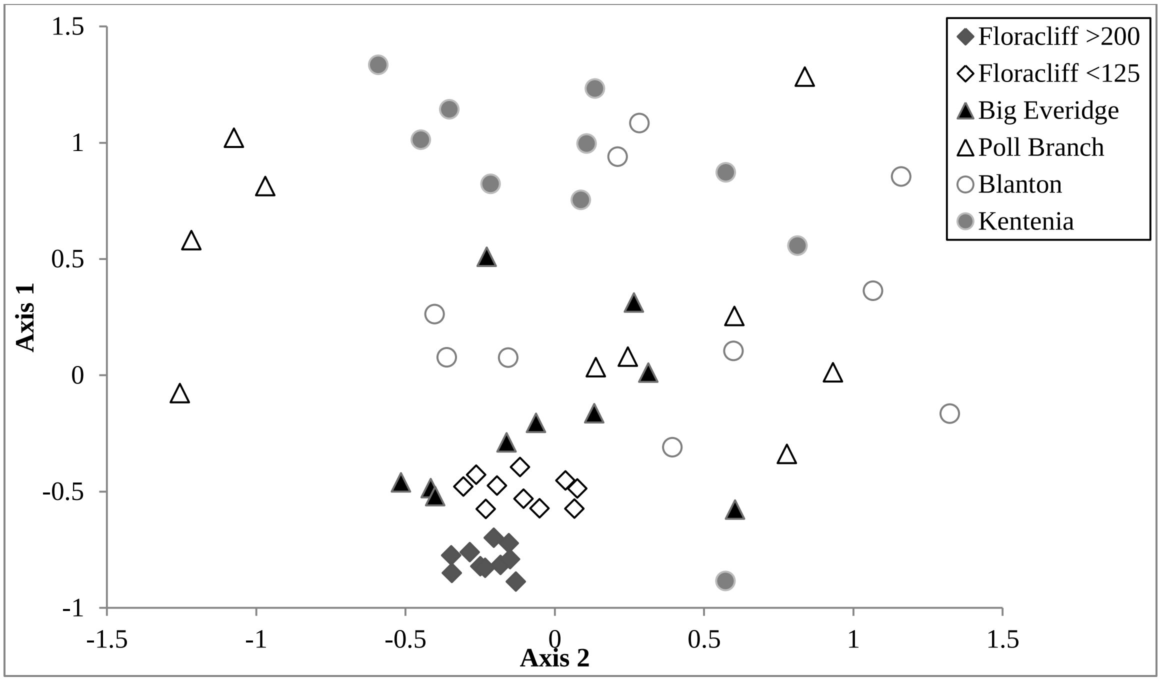

Figure 6. Land snail community structure in old-growth and second-growth forests based on Non-metric Multidimensional Scaling.

For the two groups examined (N = 30 for both), MRPP analysis revealed significant differences in the concentrations within each ($p < 0.004$, chance-corrected within-group agreement $A = 0.02$). When ecoregions were examined separately, the Inner Bluegrass showed significant differences in the concentrations ($A = 0.17$, $p < 0.001$) as did the Cumberland Plateau ($A = 0.06$, $p < 0.0001$) and Pine Mountain sites ($A < 0.001$, $p < 0.001$).

Indicator Species Analysis showed that no species were perfect indicators of either disturbance regime, when examining all ecoregions together (Table E1, APPENDIX E). However, when ecoregions were examined separately, 21 species showed affinity for old-growth (Table 3).

Table 3. Indicator species for old-growth/less disturbed conditions for three ecoregions of eastern and central Kentucky. Indicator values are presented ± standard deviation for each ecoregion.

Species	**Inner Bluegrass**	**Cumberland Plateau**	**Pine Mountain**
Carychium clappi	60 ± 2.47	65 ± 9.64	
Carychium exile	61 ± 2.66	90 ± 10.08	70 ± 10.00
Carychium nannodes	60 ± 2.27	75 ± 11.57	
Cochilocopa moreseana	70 ± 6.61	56 ± 9.20	
Collumella simplex	86 ± 7.61		
Gastrocopta armifera	85 ± 7.47		
Gastrocopta contracta	87 ± 8.25		
Gastrocopta pentodon	68 ± 8.59		
Gastrocopta procera	100 ± 9.18		
Gastrodonta interna	88 ± 7.88		
Glyphyalinia indentata	64 ± 7.18	56 ± 9.02	
Glyphyalinia wheatleyi	72 ± 8.24		
Guppya sterkii	69 ± 7.89		
Haplotrema concavum	73 ± 8.15		
Hawaii miniscula	65 ± 7.18	56 ± 9.11	
Mesomphix cupreus	70 ± 8.99		
Patera appressa		50 ± 8.82	50 ± 8.58
Punctum minutissimum		69 ± 9.54	
Striatura ferrea			
Vallonia exentrica	70 ± 8.71		
Vertigo parvula		60 ± 8.99	

Carychium exile I. Lea, 1842 had an indication of 65% toward old-growth forests ($p < 0.001$) (Table E1). This was the highest percentage among the species that were statistically significant. Conversely, *Triodopsis tridentata* (Say, 1816) showed an indication of 31% toward second-growth forests, higher than any other species when examining all ecoregions as a whole, but still not statistically significant ($p = 0.17$).

Indicator values increased considerably when calculated separately for each ecoregion area (Table E2 - E4). In the Inner Bluegrass, 16 species showed some affinity toward old-growth forests, five of which had indicator values greater than 80%, with one species *Gastrocopta procera* (Gould, 1840) having a perfect indication value (100%) (Table E2). One species in the Inner Bluegrass, *Ventridens intertextus* (A. Binney, 1841), was a statistically significant indicator of second-growth (p = 0.04). Nine species were statistically significant indicators of old-growth at the Cumberland Plateau sites, with one species, *C. exile*, having an IV = 90% (Table E3). At the Pine Mountain sites, only two species were statistically significant indicators of old-growth, and *C. exile* was again one of those species(Table E4). No species were significant indicators of second-growth in either the Cumberland Plateau or Pine Mountain ecoregion.

For analysis of relationships between snail communities and environmental factors, the first two axes of the CCA for the Inner Bluegrass ecoregion explained 32.1% of the variance within the species and environmental matrices (Figure 7 and Table D1, APPENDIX D). Monte Carlo permutation tests suggested a nearly significant relationship between habitat and snail communities present in the Inner Bluegrass (p = 0.06). Aspect, canopy cover, herbaceous cover, and soil temperature appeared to be important variables in explaining community structure within the tree stand that was > 200 years old Inner Bluegrass site, whereas shrubs 0-1m in height and duff accumulation were important variables for the high-disturbance site. Scores for each species collected are reported in Table D2. Correlations between the snail community and each of 15 environmental variables measured in the Inner Bluegrass are reported in Table D3.

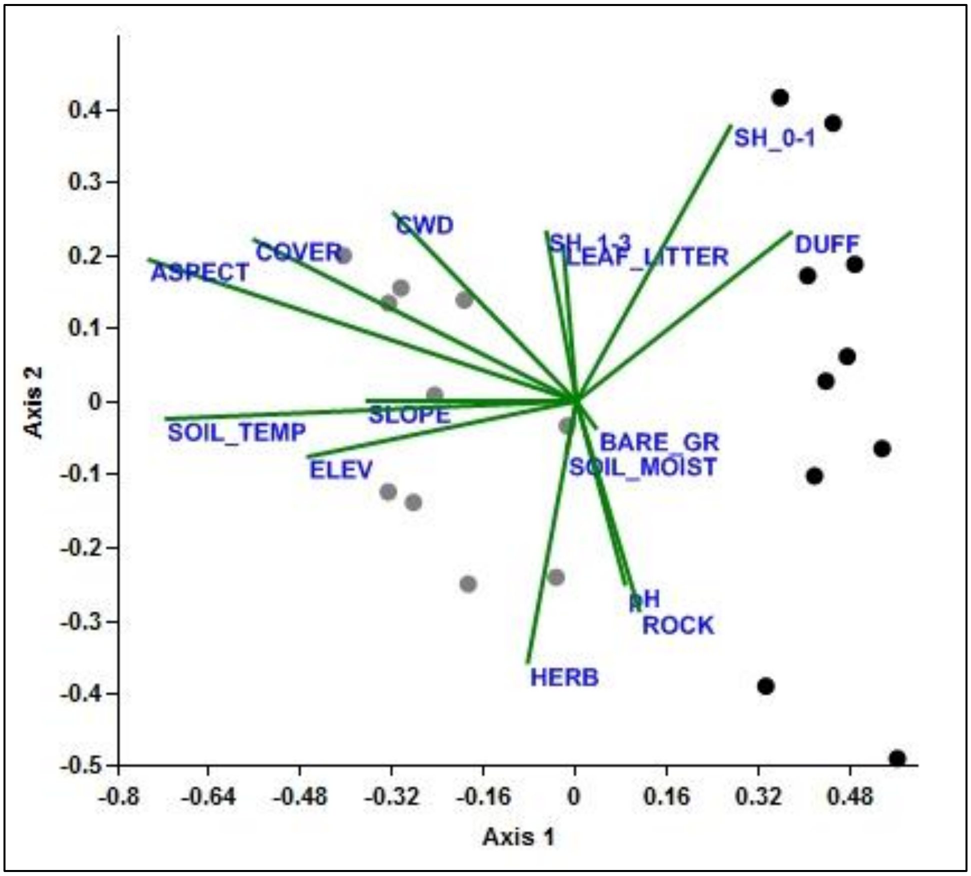

Figure 7. Canonical Correspondence Analysis of all sites sampled in the Inner Bluegrass. Sites are plotted in ordination space based on habitat parameters. Black dots represent the tree stand that is <125 years old and gray dots represent the tree stand that is > 200 years old.

The first two axes of the CCA for the Cumberland Plateau ecoregion explained 23.8% of the variance between snail species and environmental matrices (Figure 8 and Table D4). Monte Carlo permutation tests revealed no significant relationship between habitat and snail communities present on the Cumberland Plateau ($p = 0.61$). Coarse woody debris, % leaf litter, duff accumulation, canopy cover, soil moisture, and slope appeared to be important variables in explaining variation in the old-growth Cumberland Plateau site, whereas soil temperature and pH were important variables in explaining variation in the communities found in the second-growth site. Scores for each species collected are reported in Table D5. Interset correlations for the 15 environmental variables collected on the Cumberland Plateau are reported in Table D6.

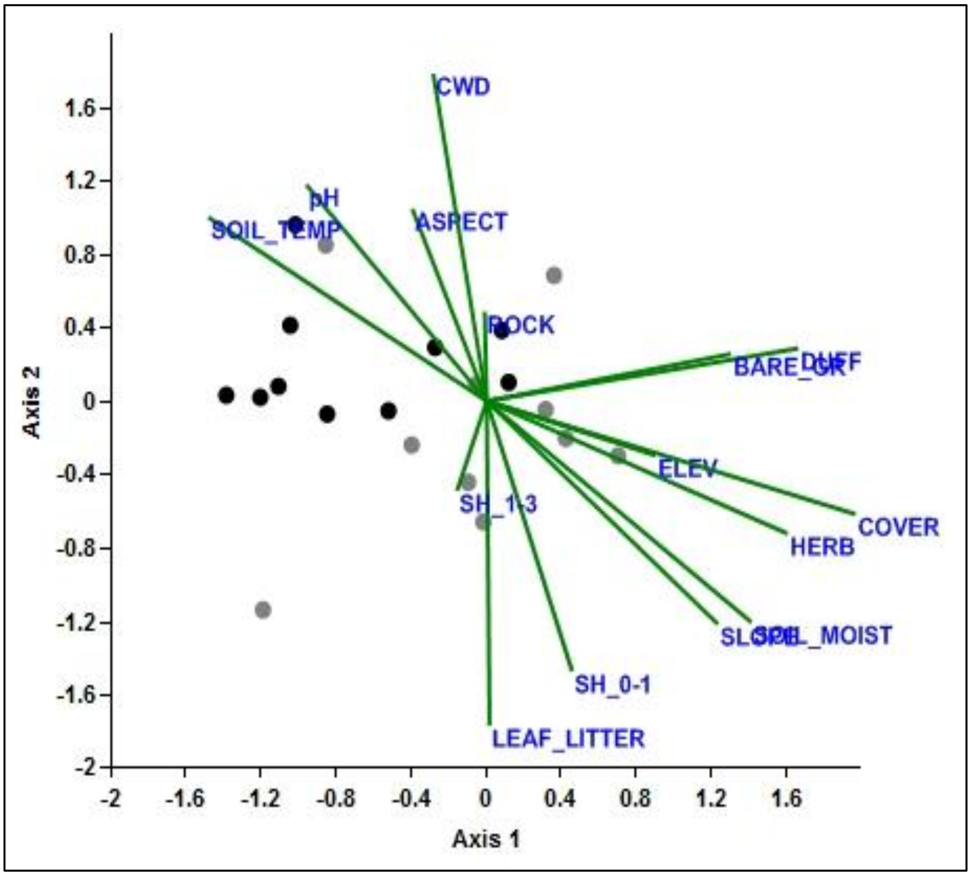

Figure 8. Canonical Correspondence Analysis of all sites sampled on the Cumberland Plateau. Sites are plotted in ordination space based on habitat parameters. Black dots represent second-growth sites and gray dots represent old-growth sites.

The first two axes of the CCA for the Pine Mountain ecoregion explained 30.1% of the variance between snail species and environmental matrices (Figure 9 and Table D7). Monte Carlo permutation tests revealed no significant relationship between habitat and snail communities present at Kentenia and Blanton Forests (p = 0.55). Canopy cover, % rock, and coarse woody debris all helped to explain variation in the snail communities within the old-growth sites found on Pine Mountain, whereas elevation, %

bare ground, soil moisture, % leaf litter, slope and pH helped to explain the variation in the communities within the second-growth site. Scores for each species collected are reported in Table D8. Interset correlations for the 15 environmental variables collected at the Pine Mountain sites are reported in Table D9.

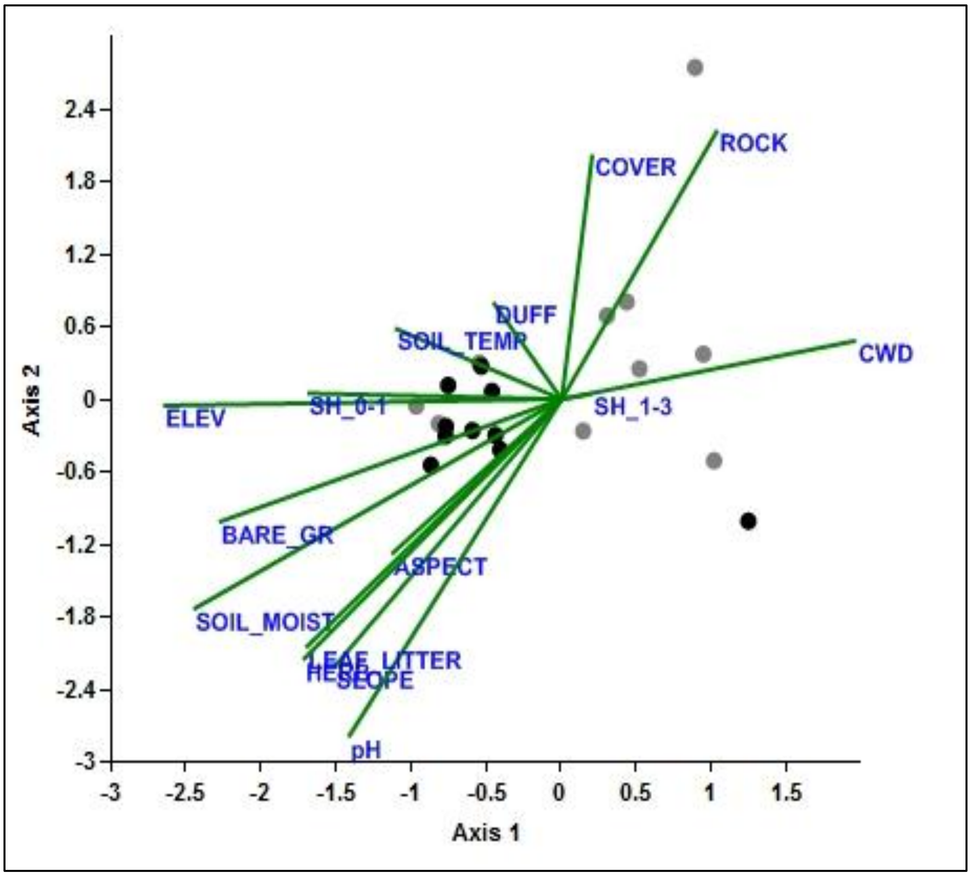

Figure 9. Canonical Correspondence Analysis of all sites sampled on Pine Mountain. Sites are plotted in ordination space based on habitat parameters. Black dots represent second-growth sites and gray dots represent old-growth sites.

CHAPTER V

DISCUSSION

The findings of this study suggest that anthropogenic disturbance affects species composition and diversity of the terrestrial gastropod communities in Kentucky. These patterns are strong enough to suggest that they may be general to the central and southern Appalachian regions. The two Inner Bluegrass communities were quite distinct, whereas the Cumberland Plateau and Pine Mountain sites differed in subtle ways between disturbance classes (Figure H1 - H3). While no single species served as a perfect indicator of undisturbed forests across the region (Table E1), 18 species were statistically significant indicators of low-disturbance forest when all regions were combined for analysis, and one species, *C. exile*, was a significant indicator in each of the three separate regional analyses. Regional variability in snail communities likely contributed to the absence of a perfect indicator. Among the 18 species that were statistically significant indicators of old-growth forest, 14 were micro-snails, indicating that micro-snails may be more reliable indicators of disturbance history than macro-snails. This suggests that micro-snails are probably more sensitive to disturbance due to their limited mobility and relatively specialized habitat requirements (Locasciulli and Boag 1987, Baur and Baur 1988). It is more difficult to explain the indicator status of the remaining four species, all of which are macro-snails: *Haplotrema concavum* Say, 1821, *Mesomphix cupreus* Rafinesque, 1831, *Mesomphix perlaevis* Pilsbry, 1900, and *Patera appressa* Say, 1821. Because of their larger size, these species should be relatively good dispersers, in relation to micro-snails, and poor indicators of forest disturbance, so this result may be a biologically un-meaningful sampling artifact. Alternatively, the indicator value of the macro-snails might be explained by life history traits of these species, which are poorly understood.

Even though several species emerged as indicators of old-growth forests on regional scales (Table 3 and Table E2 - E3), these results have to be interpreted with caution due to the fact that these species are indicators of local conditions only. Because of the high variation between ecoregions and sites, it is difficult, if not impossible, to describe a single, perfect indicator of old-growth forest. Because I continued to find new species at some sites even after 10 samples, the indicator status of some of these species may erode with additional sampling. However, the relatively low richness at high-disturbance sites and the trend towards richness reaching a plateau at all sites suggests that snails are promising taxa for finding good indicator species, perhaps more so than any previously studied group of organisms. It may be that no single species is an ideal indicator, but that the presence of several high probability indicators collectively increases confidence for inferring disturbance, particularly if these include micro-snails. This research reinforces early work by highlighting differences in disturbance sensitivity among species of land snails (Hylander et al. 2004, Kappes 2006, Kappes et al. 2009).

When comparing sites within regions, more species were good indicators of disturbance. For example, in the Inner Bluegrass, *G. procera* showed perfect indication for the less-disturbed habitat, and 15 additional species had IV greater than 80%. This suggests that within the Inner Bluegrass disturbance has played a role in shaping the community composition of the area. On the Cumberland Plateau, nine species had significant affinity for old-growth, one of which, *C. exile*, had an IV = 90%, supporting the hypothesis that disturbance affects species composition on the Cumberland Plateau.

On Pine Mountain sites, *C. exile*, again, was the higher of the two indicators found there, thus strengthening the argument that this species is a good indicator of quality habitat for eastern and central Kentucky. Due to the statistical significance found in the MRPP analysis, this also allows for the rejection of the null hypothesis that no differences exist between the disturbance regimes.

The effects of anthropogenic disturbance are moderated by other factors that may include physiographic region, the degree of disturbance, and possibly the type of disturbance. Separating these effects is challenging, and further confounded by variation in post-disturbance succession (Raheem et al. 2009), which was not quantified in this study. Though it has been shown in Kentucky that stump and root sprouts from previous forests account for much of post-clear-cut growth (Muller 1990, Arthur et al. 1997), the severity of a disturbance likely plays a crucial role in regeneration, and thus in the assemblage of organisms that inhabit a forest. A good example of this is shown at the second-growth Cumberland Plateau site, a forest that has undergone severe disturbances. Not only have localized extinctions occurred in that area, but also the availability of suitable habitat has been reduced. This has drastically altered the assemblages of land snails at that site.

According to CCA results, the composition of land snail communities in the sites studied here were tied to environmental and habitat conditions. Although the relative strength of the environmental factors varied across regions, there seemed to be a clear separation between disturbance classes, with strong correlation with environmental and habitat variables along the axis of separation. Soil moisture, pH, CWD, shrub height, duff accumulation, bare ground, and herbaceous layers all helped in explaining relationships with snail communities within at least one study area each, and these relationships provide some insight into the mechanisms underlying the separation of second-growth and old-growth snail communities. (Figure G1-G12). These environmental factors are known to be critical in shaping communities of forest snails (Kappes et al. 2006). This study reinforces and clarifies our understanding of these patterns, and further suggests that the relationships are complex in that they differ among ecoregions. Therefore, these effects are potentially driven and controlled by local conditions.

The adverse effects of anthropogenic activities on land snails that were found in this study are similar to the few studies that have been done on this subject. Reinink (1979) found that older reclaimed lands in the Netherlands supported more species than newer reclaimed lands. Cameron et al. (1980) found more snail species in British hedgerows constructed before the 20th century compared to those built since. Also, applications of herbicides on spruce plantations have been shown to alter densities of snails (Prezio et al. 1999); however, in a similar study, the effects were not detectable one year later (Hawkins et al. 1997). This suggests that the community legacy of forest management can have long-term effects on habitat availability and vegetation regeneration. Though most studies have reported negative effects of disturbance on land snails, at least one study showed increased snail abundance following disturbance, but this change was likely attributable to a change in the vegetation community following the disturbance (boreal to deciduous forests) (Strayer et al. 1986). Conversion to less complex habitats (e.g., tree plantations) can also be detrimental to snail diversity (Tattersfield et al. 2001, Bonham et al. 2002).

The results of this study indicate that community composition varied regionally across the study area. Species diversity, richness, and abundance differed among regions and disturbance classes in two of the three ecoregions studied. Evenness was similar across all ecoregions and disturbance classes, suggesting that differences in diversity are driven by species richness. NMS analysis revealed separation in community structure between disturbance classes. This separation was clearest for the Inner Bluegrass region. Sites on the Cumberland Plateau had more community overlap than the Inner Bluegrass, but showed some separation of communities between second-growth and old-growth. Sites on Pine Mountain showed more overlap than any other study area; however, the old-growth site showed a tendency for higher diversity, richness, and abundance compared to the second-growth site, suggesting possible biological significance. Strong correlations between snail communities and habitat variables were found at each of the study areas, but the specific habitat variables with high correlations differed between study areas. For instance, CWD and soil moisture were correlated with snail communities in the Cumberland Plateau and Pine Mountain ecoregion, whereas aspect and shrubs 0-1 m in height had high correlations in the Inner Bluegrass ecoregion. This suggests that relationships between snail community composition and habitat are complex and variable across the ecoregions and disturbance classes studied.

Within each ecoregion of this study, the vegetation communities differed to varying degrees (from oak-hickory to mixed mesophytic in the Inner Bluegrass and Cumberland Plateau to hemlock dominated forests on Pine Mountain). The presence of some species in old-growth sites and subsequent absence of the same species in the second-growth sites suggests that localized extinctions occurred post-disturbance (Table

B1). Although plant communities are known to indirectly influence snail community composition, (Burch 1956, 1957, Beyer and Saari 1977) this study did not find strong evidence of specific plant-snail associations. However, other factors such as post-disturbance micro-environmental conditions, canopy cover, and ground cover are more important than the plant community for controlling re-colonization (Boag 1982). In turn, the density of the vegetation can affect micro-habitat conditions for snails (Reynolds et al. 1997, Geiger et al. 2009). These micro-habitat conditions will lead to the initiation of snail locomotor activities and promote dispersal within localized areas (Boycott 1934, Boag 1985, Prior 1985). Adverse climatic conditions (e.g., drought) following disturbance can adversely affect micro-habitat and cause local extinctions, which may have played a role within the second-growth forest studied here (Chang and Emlen 1993). Disturbances, followed by adverse climate conditions would lead to slow recovery of land snail communities. Bormann and Likens (1979) suggested that micro-environmental conditions recover rapidly following disturbances in northern New England, but in the southeastern United States, disturbance can have strong and lasting effects on leaf litter parameters, herbaceous layer recovery, and CWD (Ash 1995, Meier et al. 1995, Webster and Jenkins 2005). These habitat parameters will influence species composition and potential to re-colonize an area (Hawkins et al. 1998, Barker and Mayhill 1999, Martin and Sommer 2004). Leaf litter, herbaceous cover, and CWD will also affect desiccation rates of land snails which will determine presence or absence of a species (Asami 1993).

The differences between disturbance regimes and ecoregions in terms of diversity, richness, and abundance of snails described in this study are likely related to the substrate and forest composition. The Inner Bluegrass is underlain by limestone, whereas the other two study areas are composed primarily of sandstone. Because land snails require calcium sources for basic physiological and biological processes (Fournié and Chétail 1984) and it is known that calcium availability effects the presence of land snails (Wareborn 1992, Johannessen and Solhoy 2001, Hotopp 2002, Skeldon et al. 2007), limestone areas typically have relatively high abundances of snails (Schilthuizen et al. 2003, Dourson and Beverly 2008, Jurickova et al. 2008). This helps explain the high abundance of snails at the Inner Bluegrass sites. However, a site does not require limestone geology for high species richness. For example, in this study, a site with sandstone geology, the old-growth Cumberland Plateau site (Lilley Cornett Woods) had more species (N = 54) than the Inner Bluegrass region (N = 50) (Figure 1). The relatively high diversity at this site is most likely driven by favorable biotic factors and heterogeneous micro-climatic conditions. Most of the sampling points in the Cumberland Plateau were located in cove hardwood forests (Martin 1975). Some tree species in these forests, including Flowering Dogwood (*Cornus florida* L.), act as sources of calcium and play a role in its cycling through an ecosystem (Nation 2007). This may indirectly drive diversity and abundance of land snails.

Vegetation may also be a primary factor behind the relatively low snail diversity in the Pine Mountain region. The Pine Mountain sampling sites were dominated by eastern hemlock (*Tsuga canadensis* L.), a forest community type that generally has low calcium availability (Figure 2-4). Low calcium availability is probably one important factor driving the relatively low diversity and abundance at these sites; however some species, such as *M. perlaevis* and *Glyphyalinia* spp., are specialists in these conditions and are generally found in higher abundances in these areas (Nekola 2010). Because of the expected loss of hemlock trees as the invasive Hemlock Woolly Adelgid, *Adelges tsugae* (Annand, 1928), spreads across eastern and central Kentucky, the snail community in these forests may change in coming decades. Although snail diversity may increase locally (i.e. alpha diversity) as hemlocks are replaced, diversity between communities (beta diversity) will become virtually non-existent due to the homogenization of habitats, and regional diversity (gamma diversity) will be negatively affected. Similar predictions have been made for the effects of hemlock loss on arthropod communities (Rohr et al. 2009). Limited sampling in the hemlock forests may have made differences between second-growth and old-growth provisional. It may be that species inhabiting hemlock-dominated stands are more tolerant than species in hardwood-dominated forests. Because of this, they may be better adapted to disturbance, making them able to re-colonize quicker than species that inhabit hardwood forests. Of course this relies on whether or not the forest that succeeds the previous forest is similar to what was present pre-disturbance.

Conservation and Management Implications

Previous research on land snails has often focused on ecological processes in which snails may be detrimental to other organisms. This study highlights the high regional biodiversity of land snails in eastern and central Kentucky, and the utility of land snails as indicators of habitat disturbance. The results reported here indicate that land snails, especially micro-snails, are particularly sensitive to changes associated with human-caused disturbance. The two sites with the highest levels of disturbance, Floracliff < 125 years old (Inner Bluegrass) and Poll Branch (Cumberland Plateau), showed the strongest differences in communities and species when compared to paired sites of low-disturbance. This suggests that community changes are proportional to levels of disturbance. Also, it is possible that disturbance in adjacent habitats could have ecological consequences within a forest such as creating corridors for invasive species of plants and animals to invade an intact forest, thus altering the habitats and community composition within that forest (Baur and Erhardt 1995). Disturbance may also create opportunities for establishment and expansion of exotic species to enter ecosystems, thus researchers should monitor for invasions following disturbance (Kalisz and Dotson 1989, Hendrix and Bohlen 2002, Kappes 2006).

Land snails may be a good study group to better understand how anthropogenic activities shape species presences in an ecosystem. The creation of roads and trails in forested areas reduces salamander and macroarthropod abundances within close proximity. This has also been observed in land snails (Dourson pers. comm.), but more work is needed to understand how anthropogenic disturbances, including peripheral events, affect communities.

Land snails are an important foundational component of terrestrial ecosystems and can be considered among the most important organisms for carrying out essential forest ecosystem functions. Unfortunately, the attention paid to land snails has often focused on ecological processes that are detrimental to other organisms. For example, land snails carry the Meningeal Worm (*Parelaphostrongylus tenius* Dougherty, 1945) and infect cervids such as white-tailed deer, elk, and moose which may lead to mortality (Anderson 1962, 1972, Wasel 1995, Boppel 1998, Suominen et al. 1999, Alexy 2004), though it is a naturally occurring parasite. Conversely, overpopulations of cervids play a role in disturbing forest floor vegetation, thus altering the distribution and composition of forest floor dwelling fauna and flora (Suominen 1999, Pedersen and Wallis 2004, Webster et al. 2005, Griggs et al. 2006, Tanentzap et al. 2011). Future research should focus on examining how cervid overpopulation affects other organisms rather than how these organisms effect a very plentiful and unthreatened group of animals.

The contribution of snails to maintaining properly functioning forests is poorly understood. For instance, in forestry practice, green tree retention may sustain ecological integrity and maintain biodiversity (Hylander et al. 2004, Rosenvald and Lõhmus 2008, Abele 2010). A mixed strategy of forest management that considers age of stand rotation as well as the scale at which forested areas are managed may be required to maintain biodiversity and prevent species extirpations. This concept is demonstrated in the Inner Bluegrass site with the stand that was > 200 years. The Inner Bluegrass study sites were selectively logged at the turn of the 20th century. The presence of older trees in those areas may have helped to maintain the land snail diversity, richness, and abundances present. Land snails may face extinctions in forests that are managed for timber resources. Because of this, forests that are undisturbed may harbor high land snail diversity as well as other organisms. Thus, these areas may represent unique areas important for preserving biological diversity. Old-growth forests can also serve as control areas that illustrate species composition in the absence of disturbance. This highlights and strengthens the arguments for the high value of old-growth in terms of scientific research and historical significance (Whitney 1987).

Dispersal from refugia following a disturbance is another important process affecting snail community composition. In areas with severe and repeated disturbances, such as Poll Branch (the second-growth site on the Cumberland Plateau), refugia are likely limited. In the habitats studied here, likely refugia included: CWD, rock talus, or nearby forest patches that escaped disturbance (Jacot 1935). Rock talus is effective refugia for both plants and land snails from deer browsing and fire (Kiss and Magnin 2003, Carson et al. 2005, Comisky et al. 2005). Patches of bryophytes can also serve as refuge for land snails during logging events (Hylander et al. 2004). The rate of re-colonization of disturbed areas from refugia is poorly understood, but the frequency and severity of disturbance are likely important (Kiss et al. 2004). Repeated disturbances may create small, isolated populations with limited gene flow, which may lead to localized extinctions when coupled with stochastic events. Habitat left within the disturbed areas may not be suitable for populations to survive. This could also lead to localized extinctions (Hylander et al. 2005). If no refugia are present, those individuals left have nowhere to turn for protection. Species will likely become extirpated from an area and re-colonization will depend upon dispersal from surrounding undisturbed forests. Again, community composition and structure of re-colonizing species will depend heavily on vegetation and environmental conditions present post-disturbance.

In the central hardwood forest, the dominant natural disturbance regime is canopy gaps created by tree falls due to wind or by natural die off of single or small patches of trees (Runkle 1981, 1982, Runkle and Yetter 1987). These natural gaps have relatively short-term and low impact on most animal communities because the soil and micro-habitats remain intact relative to most types of anthropogenic disturbance. Management practices that mimic these small openings with minimal disturbance to the soil and other beneficial habitat characteristics, such as CWD and leaf litter, will leave potential refugia for snails and increase the probability that an area will be re-colonized. This would also allow for species of plants and animals to become re-established several decades earlier than they would if a larger disturbance were to move through a forest (Runkle 1991).

Old-growth forests provide a reference to examine the structure and composition of forests as they existed prior to European settlement (Leopold 1941). To maintain ecological integrity and diversity, the remaining old-growth forests should be located, described, and protected. Though it would be difficult to recreate or restore many of the characteristics of old-growth forests (age structure, diversity of genetics, pit and mound topography), some features can be managed such as leaving CWD intact and creating small canopy gaps (Runkle 1991). Appropriate management would provide suitable habitat and promote re-colonization for many species Land managers should make efforts to manage forests with minimal impact as well as try to mimic the characteristics of old-growth forest.

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APPENDIX A: PLANT SPECIES PRESENT AT EACH STUDY SITE.

Table A1. Tree and shrub species found at each study site. Basal areas in meters^2 per hectare ± SE are shown for species surveyed during vegetation analysis. Tree species not surveyed, but can be found at the study site are denoted by X.

		Ecoregion		
Species	**Common Name**	**Inner Bluegrass**	**Cumberland Plateau**	**Pine Mountain**
ACERACEAE				
Acer negundo L.	Box Elder	X	X	X
Acer pensylvanicum L.	Striped Maple		X	X
Acer rubrum L.	Red Maple	0.57 ± 0.47	2.64 ± 0.77	X
Acer saccharum L.	Sugar Maple	6.54 ± 1.13	4.24 ± 1.04	2.98 ± 0.53
ANACARDIACEAE				
Rhus copallina L.	Winged Sumac	X	X	X
Rhus glabra L.	Smooth Sumac	X	X	X
ANNONACEAE				
Asimina triloba L.	Paw Paw	X	X	X
BETULACEAE				
Betula lenta L.	Sweet Birch		X	X
Carpinus carolinia Walt.	American Hornbeam	X	X	X
Ostrya virginiana Mill.	Hop-hornbeam	X	X	X
CAPRIFOLIACEAE				
Lonicera spp.	Honeysuckle	X	X	X
Viburnum acerifolium L.	Mapleleaf Viburnum		X	X
CELASTRACEAE				
Euonymus americanus L.	Strawberry-bush	X	X	X
CORNACEAE				
Cornus alternifolia L.	Alternate-leafed Dogwood	X	X	
Cornus florida L.	Flowering Dogwood	0.11 ± 0.11	X	X

Table A1. (Continued)

Species	Common Name	Ecoregion Inner Bluegrass	Ecoregion Cumberland Plateau	Ecoregion Pine Mountain
CUPRESSACEAE				
Juniperus virginiana L.	Red-cedar	4.36 ± 0.95	X	
ERICACEAE				
Gaylussacia baccata Wang.	Huckleberry		X	X
Kalmia latifolia L.	Mountain Laurel		X	X
Oxydendron arboreum L.	Sourwood	X	0.23 ± 0.23	0.46 ± 0.27
Rhododendron calendulaceum Michx.	Flame Azalea		X	X
Rhododendron cumberlandesnse E.L.Br.	Cumberland Azalea		X	X
Rhododendron maximum L.	Rosebay Rhododendron		X	X
Vaccinium corymbosum L.	High-bush Blueberry		X	X
Vaccinium stamineum L.	Deerberry		X	X
Vaccinium pallidum Aiton.	Low-bush Blueberry		X	X
FABACEAE				
Cercis canadensis L.	Redbud	X	X	X
Robinia psuedoacia L.	Black Locust	X	0.11 ± 0.11	0.11 ± 0.11
FAGACEAE				
Castanea dentate Marsh.	American Chestnut		X	X
Fagus grandifolia Ehrh.	American Beech		0.11 ± 0.11	4.13 ± 1.02
Quercus alba L.	White Oak	0.46 ± 0.46	0.92 ± 0.60	0.34 ± 0.19
Quercus coccinea Muenchh.	Scarlet Oak	X	X	X
Quercus falcata Michx.	Southern Red Oak	X	X	X
Quercus miralandica Muenchh.	Black Jack Oak	X	X	X
Quercus muehlenbergii Eng.	Chinquapin Oak	6.89 ± 1.05	X	X

Table A1. (Continued)

		Ecoregion		
Species	**Common Name**	**Inner Bluegrass**	**Cumberland Plateau**	**Pine Mountain**
Quercus montana L.	Chestnut Oak	0.11 ± 0.11	0.69 ± 0.38	7.12 ± 1.53
Quercus rubra L.	Northern Red Oak	2.18 ± 0.79	1.72 ± 0.68	2.98 ± 0.94
Quercus stellata Wang.	Post Oak	0.26 ± 0.16	X	X
Quercus velutina Lam.	Black Oak	2.07 ± 0.70	0.11 ± 0.11	0.92 ± 0.51
HAMAMELIDACEAE				
Hamamelis virginiana L.	Witch Hazel	X	X	X
Liquidambar styraciflua L.	Sweet Gum	X	X	X
HIPPOCASTANACEA				
Aesculus flava Aiton.	Yellow Buckeye		0.34 ± 0.34	X
Aesculus glabra Wild.	Ohio Buckeye	0.34 ± 0.19	X	
JUGLANDACEAE				
Carya cordiformis Wang.	Bitternut Hickory	X	X	X
Carya glabra Mill.	Pignut Hickory	0.69 ± 0.29	X	X
Carya ovalis Wang.	Red Hickory	X	X	X
Carya ovata Mill.	Shagbark Hickory	1.15 ± 0.61	0.34 ± 0.34	0.11 ± 0.11
Carya spp.	Hickory spp.		7.42 ± 5.73	1.15 ± 0.39
Carya tomentosa Nutt.	Mockernut Hickory	X	X	X
Juglans cinera L.	Butternut		X	X
Juglans nigra L.	Black Walnut	0.46 ± 0.27	0.11 ± 0.11	X
LAURACEAE				
Lindera benzoin L.	Spicebush		X	X
Sassafras albidum Nutt.	Sassafras	X	0.11 ± 0.11	0.11 ± 0.11
MAGNOLIACEAE				

Table A1. (Continued)

Species	**Common Name**	**Ecoregion** **Inner Bluegrass**	**Ecoregion** **Cumberland Plateau**	**Ecoregion** **Pine Mountain**
Liriodendron tulipifera L.	Yellow Poplar	X	4.94 ± 1.56	3.56 ± 1.17
Magnolia acuminata L.	Cucumber Tree		X	X
Magnolia macrophylla Michx.	Bigleaf Magnolia	X	0.11 ± 0.11	0.69 ± 0.47
Magnolia tripetala L.	Umbrella Tree		X	X
MORACEAE				
Morus rubra L.	Reb Mullberry		X	X
NYSSACEAE				
Nyssa sylvatica Marsh.	Black Gum	0.92 ± 0.35	0.23 ± 0.16	0.23 ± 0.16
OLEACEAE				
Fraxinus americana L.	White Ash	X	X	X
Fraxinus pennsylvanicus L.	Green Ash	1.61 ± 0.94	X	0.11 ± 0.11
PINACEAE				
Pinus echinata Mill.	Shortleaf Pine		X	X
Pinus rigida Mill.	Pitch Pine		X	X
Pinus virginiana Mill.	Virginia Pine	X	X	X
Tsuga canadensis L.	Eastern Hemlock		X	3.33 ± 1.34
PLATANACEAE				
Platunus occidentals L.	Sycamore	0.11 ± 0.11	X	X
ROSACEAE				
Amelanchier arborea Michx.	Serviceberry		0.11 ± 0.11	X
Prunus serotina Ehrh.	Black Cherry		3.90 ± 3.43	0.91 ± 0.34
SANTALACEAE				
Pyrularia pubera Michx.	Oil Nut		X	X

Table A1. (Continued)

		Ecoregion		
Species	**Common Name**	**Inner Bluegrass**	**Cumberland Plateau**	**Pine Mountain**
SAXIFRAGACEAE				
Hydrangea arborescens L.	Wild Hydrangea		X	
TILIACEAE				
Tillia heterophylla Vent.	American Basswood	1.26 ± 0.54	1.15 ± 0.51	0.92 ± 0.51
ULMACEAE				
Ulmus americana L.	American Elm	0.11± 0.11	X	
Ulmus rubra Muhl.	Slippery Elm		X	

APPENDIX B: LAND SNAIL SPECIES FOUND AT EACH STUDY SITE.

Table B1. Species of land snails collected during the duration of this study. Study areas are broken down by ecoregion and then further broken down by specific site. FC < 125 = tree stand at Floracliff State Nature Preserve with trees less than 125 years old, FC > 200 = tree stand at Floracliff State Nature Preserve with trees greater than 200 years old, PB = Poll Branch (second-growth), LCW = Lilley Cornett Woods (old-growth), KSF = Kentenia State Forest (second-growth), and BSNP = Blanton Forest State Nature Preserve (old-growth). The presence of a species at a particular site is denoted by X.

	Ecoregion					
	Inner Bluegrass		**Cumberland Plateau**		**Pine Mountain**	
Species	**FC < 125**	**FC > 200**	**PB**	**LCW**	**KSF**	**BSNP**
CARYCHIIDAE						
Carychium clappi Hubricht, 1959	X	X	X	X	X	X
Carychium exile I. Lea, 1842	X	X	X	X		X
Carychium nannodes G.H. Clapp, 1905	X	X	X	X	X	X
COCHILICOPIDAE						
Cochilicopa moreseana (Doherty, 1878)	X	X	X	X	X	X
DISCIDAE						
Anguispira alternata (Say, 1816)	X	X				
Anguispira kochi (Pfeiffer, 1821)	X	X				
Anguispira mordax (Shuttleworth, 1852)			X	X	X	
Discus patulus (Deshayes, 1830)	X	X	X		X	X
HAPLOTREMATIDAE						
Haplotrema concavum (Say, 1821)	X	X	X	X		X
HELICARNIDAE						
Euconulus fulvus (Muller, 1774)	X	X		X		
Guppya sterkii (Dall, 1888)	X	X		X		
HELICODISCIDAE						
Helicodiscus notius Hubricht, 1962	X	X	X			
PHILOMYCIDAE						

Table B1. (Continued)

	Ecoregion					
	Inner Bluegrass		Cumberland Plateau		Pine Mountain	
Species	**FC < 125**	**FC > 200**	**PB**	**LCW**	**KSF**	**BSNP**
Palifera dorsalis (A. Binney, 1885)				X		X
Philomycus carolinensis (Bosc, 1802)						X
POLYGYRIDAE						
Appalachina sayana (Pilsbry, 1906)	X	X	X	X	X	X
Euchemotrema fraternum (Say, 1824)	X	X	X	X	X	X
Inflectarius inflectus (Say, 1821)	X			X		
Inflectarius rugeli (Shuttleworth, 1852)	X	X	X	X	X	X
Mesodon elevatus (Say, 1821)	X	X				
Mesodon normalis (Pilsbry, 1900)			X	X	X	X
Mesodon thyroidus (Say, 1816)	X	X				
Mesodon zaleatus (A. Binney, 1837)	X	X		X		
Patera appressa (Say, 1821)	X	X		X		X
Stenotrema angellum Hubricht, 1958	X	X				
Stenotrema barbatum (G.H. Clapp, 1904)	X	X				
Stenotrema stenotrema (Pfeiffer, 1842)	X	X	X	X	X	X
Neohelix albolarbis (Say, 1816)	X	X		X		
Tridopsis sp.				X		
Triodopsis tridentata (Say, 1816)	X	X	X	X	X	X
Xolotrema denotatum (Ferussac, 1821)	X	X	X	X		X
POMATIOPSIDAE						
Pomatiopsis lipadaria (Say, 1817)	X	X	X	X		X
PUNCTIDAE						

Table B1. (Continued)

	Ecoregion					
	Inner Bluegrass		Cumberland Plateau		Pine Mountain	
Species	**FC < 125**	**FC > 200**	**PB**	**LCW**	**KSF**	**BSNP**
Punctum minutissimum (I. Lea, 1841)	X	X	X	X	X	X
Punctum blandianum (Pilsbry, 1900)				X		
PUPILLIDAE						
Columella simplex (Gould, 1841)	X	X		X		
Gastrocopta armifera (Say, 1821)	X	X		X		
Gastrocopta contracta (Say, 1822)	X	X		X	X	
Gastrocopta contricaria (Say, 1816)				X		
Gastrocopta pentodon (Say, 1821)	X	X		X		
Gastrocopta procera (Gould, 1840)	X					
Pupoides albilabris (C.B. Adams, 1841)	X	X		X		
Vertigo bollesiana(E.S. Morse, 1875)			X	X	X	X
Vetigo gouldii (A. Binney, 1843)				X		
Vertigo parvula Sterki, 1890	X			X		
Vertigo tridentata Wolf, 1870	X	X				
STROBILSOPSIDAE						
Stobilops aenea Pilsbry, 1926	X	X		X		
Strobilops labyrinthica (Say, 1817)	X	X				
SUCCINEIDAE						
Catinella oklahomarum (Webb, 1953)	X	X				
VALLONIADAE						
Vallonia excentrica Sterki, 1893	X					
ZONITIDAE						

Table B1. (Continued)

	Ecoregion					
	Inner Bluegrass		Cumberland Plateau		Pine Mountain	
Species	**FC < 125**	**FC > 200**	**PB**	**LCW**	**KSF**	**BSNP**
Gastrodonta interna (Say, 1822)	X	X		X	X	
Glyphyalinia cryptomphala (G.H. Clapp, 1915)				X		
Glyphyalinia indentata (Say, 1823)	X	X	X	X	X	X
Glyphyalinia wheatleyi (Bland, 1883)	X	X	X	X	X	X
Hawaii miniscula (A. Binney, 1840)	X	X	X	X	X	X
Mesomphix cupreus (Rafinesaue, 1831)	X				X	
Mesomphix inornatus (Say, 1821)	X	X	X	X	X	X
Mesomphix perlaevis (Pilsbry, 1900)	X	X		X		X
Paravitrea capsella (Gould, 1851)	X	X	X	X	X	X
Paravitrea placentula (Shuttleworth, 1852)				X		
Striatura meridionalis (Pilsbry and Ferriss, 1906)	X			X		
Striatura ferrea E.S. Morse, 1864				X		
Ventridens demissus (A. Binney, 1843)				X	X	X
Ventridens gularis (Say, 1822)			X	X	X	X
Ventridens intertextus (A. Binney, 1841)	X	X				
Ventridens lasmodon (Phillips, 1841)			X	X	X	X
Ventridens lawae (W.G. Binney, 1892)				X		
Ventridens ligera (Say, 1821)	X	X	X			X
Ventridens theloides (Walker and Pilsbry, 1902)				X		
Zonitoides arboreus (Say, 1816)	X	X		X		X
Zonitoides elliotti (Redfield, 1856)				X		

APPENDIX C: COUNTY RECORDS AND BIOGEOGRAPHICAL AFFINITIES

Table C1. County records found during the course of this study with status and biogeographical affinities. Keys to this table are as follows: **Status**: CO = Common, LR = Limited Range, RA = Rare, E = KSNPC listed as Endangered. **Affinity**: CP = Cumberland Plateau, GRSM = Great Smoky Mountains, NOR = Northern species, WIDE = Wide ranging species, WVV = West Virginia/Virginia. New county records are denoted by an X in the column underneath the county.

			County Record		
Species	**Status**	**Affinity**	**Fayette**	**Letcher**	**Harlan**
CARYCHIIDAE					
Carychium clappi Hubricht, 1959	CO	GRSM	X		
Carychium exile I. Lea, 1842	CO	WIDE	X		
Carychium nannodes G.H. Clapp, 1905	CO	WIDE	X		
COCHILOCOPIDAE					
Cochilocopa moreseana (Doherty, 1878)	CO	WIDE	X		
DISCIDAE					
Anguispira Kochi (Pfeiffer,1821)	CO	WIDE	X		
Discus patulus (Deshayes, 1830)	CO	WIDE	X		
HELICARIONIDAE					
Euconulus fulvus (Muller, 1774)	CO	NOR			
Guppya sterkii (Dall, 1888)	CO	WIDE	X		
HELICODISCIDAE					
Helicodiscus notius Hubricht, 1962	CO	WIDE	X		
PHILOMYCIDAE					
Palifera dorsalis (A. Binney, 1885)	CO	NOR			X
Philomycus carolinensis (Bosc, 1802)	CO	WIDE		X	
POLYGYRIDAE					
Appalachina sayana (Pilsbry, 1906)	CO	CP	X		
Euchemotrema fraternum (Say, 1824)	CO	WIDE	X		

Table C1. (Continued)

				County Record	
Species	**Status**	**Affinity**	**Fayette**	**Letcher**	**Harlan**
Inflectarius rugeli (Shuttleworth, 1852)	CO	WIDE			X
Mesodon elevates (Say, 1821)	CO	WIDE	X		
Mesodon normalis (Pilsbry, 1900)	LR	GRSM			
Mesodon zaleatus (A. Binney, 1837)	CO	WIDE		X	
Neohelix albolabris (Say, 1816)	CO	WIDE		X	
Triodopsis tridentata (Say, 1816)	CO	WIDE	X		
Patera appressa (Say, 1821)	CO	WIDE	X		
Xolotrema denotatum (Ferussac, 1821)	CO	WIDE	X		
PUNCTIDAE					
Punctum blandianum (Pilsbry, 1900)	LR	GRSM		X	
Punctum minutissimum (I. Lea, 1841)	CO	WIDE	X	X	
PUPILLIDAE					
Collumella simplex (Gould, 1841)	CO	WIDE	X		
Gastrocopta armifera (Say, 1821)	CO	WIDE	X	X	
Gastrocopta contracta (Say, 1822)	CO	WIDE	X		
Gastrocopta contricaria (Say, 1816)	CO	WIDE		X	
Gastrocopta pentodon (Say, 1821)	CO	WIDE	X		
Gastrocopta procera (Say, 1821)	CO	WIDE	X		
Pupoides albilabris (C.B. Adams, 1841)	CO	WIDE	X	X	
Vertigo bollesiana (E.S. Morse, 1875)	E	NOR		X	
Vertigo parvula Sterki, 1890	RA	WVV		X	
Vetigo gouldii (A. Binney, 1843)	CO	NOR		X	
Vertigo tridentata Wolf, 1870	CO	WIDE	X		

Table C1. (Continued)

Species	Status	Affinity	County Record		
			Fayette	Letcher	Harlan
STROBILOPSIDAE					
Strobilops aeneus Pilsbry, 1926	CO	WIDE	X	X	
Strobilops labyrinthica (Say, 1817)	CO	WIDE	X		
SUCCINEIDAE					
Catinella oklahomarum (Webb, 1953)	CO	WIDE	X		
VALLONIADAE					
Vallonia exentrica Sterki, 1893	CO	WIDE	X		
ZONITIDAE					
Gastrodonta interna (Say, 1822)	CO	WIDE	X	X	
Glyphyalinia cryptomphala (G.H. Clapp, 1915)	CO	WIDE		X	
Glyphyalinia indentata (Say, 1823)	CO	WIDE	X		
Glyphyalinia wheatleyi (Bland, 1883)	CO	WIDE		X	
Hawaii miniscula (A. Binney, 1840)	CO	WIDE	X		
Mesomphix cupreus (Rafinesque, 1831)	CO	NOR	X		
Mesomphix inornatus (Say, 1821)	CO	NOR	X		
Mesomphix perlaevis (Pilsbry, 1900)	CO	WIDE	X		
Mesomphix vulgatus H. B. Baker, 1933	CO	WIDE	X		
Striatura ferrea E.S. Morse, 1864	LR, RA	NOR			
Striatura meridionalis (Pilsbry and Ferriss, 1906)	CO	WIDE	X		
Ventridens gularis (Say, 1822)	CO	WIDE		X	
Ventridens ligera (Say, 1821)	CO	WIDE			X
Ventridens lasmodon (Phillips, 1841)	LR	GRSM			
Ventridens lawae (W.G. Binney, 1892)	LR	GRSM			

Table C1. (Continued)

			County Record		
Species	**Status**	**Affinity**	**Fayette**	**Letcher**	**Harlan**
Zonitoides arboreus (Say, 1816)	CO	WIDE		X	
Zonitoides elliotti (Redfield, 1856)	LR	GRSM		X	

APPENDIX D: CANONICAL CORRESPONDENCE ANALYSIS TABLES FOR EACH SAMPLED ECOREGION.

Table D1. Axis summary statistics for the Inner Bluegrass ecoregion.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalue	0.11	0.04	0.03
Variance in species data			
% of variance explained	22.70	9.40	7.80
Cumulative % explained	22.70	32.10	39.90
Pearson Correlation Spp-Env*	0.98	0.98	0.97
Kendall (Rank) Corr. Spp-Env	0.83	0.92	0.84

Table D2. Species Scores and raw data totals for the Inner Bluegrass ecoregion.

Species	**Axis 1**	**Axis 2**	**Axis 3**	**Raw Data Totals**
Anguispira alternata	2.14	-2.32	-0.41	34
Anguispira kochi	0.72	1.73	-0.48	54
Appalachina sayana	0.66	2.16	0.01	51
Carychium clappi	0.32	-0.12	0.22	236
Carychium exile	0.26	-0.66	-0.61	243
Carychium nannodes	0.30	0.60	-0.07	233
Catinella oklahomarum	-0.28	0.42	0.25	19
Cochilocopa moreseana	-0.71	0.01	1.35	50
Collumella simplex	-1.19	-0.39	0.84	70
Discus patulus	-0.21	-0.65	-0.40	32
Euchemotrema fraternum	-0.16	1.60	0.60	42
Euconulus fulvus	1.46	-0.07	-0.91	20
Gastrocopta armifera	-1.08	-0.81	-1.98	78
Gastrocopta contracta	-1.41	-0.06	-1.28	79
Gastrocopta pentodon	-0.52	-0.30	1.22	45
Gastrocopta procera	-2.34	0.36	0.49	71
Gastrodonta interna	-1.39	-1.15	-0.14	78
Glyphyalinia indentata	-0.53	-0.29	0.32	38
Glyphyalinia wheatleyi	-1.24	1.14	-0.99	41
Guppya sterkii	-0.77	1.18	-1.21	34
Haplotrema concavum	-0.82	-1.26	1.93	43
Hawaii miniscula	-0.42	0.68	0.54	51
Helicodiscus notius	0.58	-0.29	2.91	22
Inflectarius inflectus	1.47	1.62	0.83	22
Inflectarius rugeli	0.46	0.33	0.18	17
Mesodon elevatus	0.81	-0.66	0.11	26
Mesodon thyroidus	0.71	-0.11	-1.48	20
Mesodon zaleatus	0.03	-1.22	-2.54	20
Mesomphix cupreus	-2.32	-0.70	3.17	16

Table D2. (Continued)

Species	Axis 1	Axis 2	Axis 3	Raw Data Totals
Mesomphix inornatus	0.72	0.97	0.90	23
Mesomphix perlaevis	0.49	1.10	0.13	31
Neohelix albolabris	1.00	-0.02	2.20	19
Paravitrea capsella	-0.09	0.92	-1.33	18
Patera appressa	0.37	-1.05	0.47	28
Pomatiopsis lipadaria	0.22	-0.71	2.08	15
Punctum minutissimum	1.28	0.41	1.08	22
Pupoides albilabris	0.84	2.23	-1.48	13
Stenotrema angellum	1.97	-2.13	0.38	16
Stenotrema barbatum	1.13	0.26	2.26	14
Stenotrema stenotrema	0.58	1.24	-1.00	12
Striatura meridionalis	0.26	-1.55	-1.33	30
Strobilops aenea	0.69	1.83	1.24	19
Strobilops labyrinthica	0.65	-1.96	0.68	15
Triodopsis tridentata	2.67	-3.19	0.81	16
Vallonia exentrica	-2.40	0.62	0.51	12
Ventridens intertextus	2.83	1.36	-1.80	15
Ventridens ligera	1.05	0.84	-0.82	21
Vertigo tridentata	0.49	1.28	0.50	32
Xolotrema denotatum	1.86	-1.76	0.87	20
Zonitoides arboreus	1.50	-0.27	-0.72	19

Table D3. Inter-set correlations for the 15 environmental variables collected in the Inner Bluegrass ecoregion.

	Correlations		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Elevation	-0.49	-0.08	-0.21
Slope	-0.35	0.02	0.15
Aspect	-0.75	0.11	0.26
pH	0.03	-0.24	0.31
Soil Temperature	-0.70	-0.04	0.10
Soil Moisture	-0.00	-0.04	-0.24
Duff	0.43	0.37	-0.07
Canopy Cover	-0.61	0.12	0.07
Leaf Litter	-0.04	0.20	0.34
Bare Ground	0.05	-0.12	-0.25
Rock	0.12	-0.22	-0.11
CWD	-0.31	0.28	-0.14

Table D3. (Continued)

	Correlations		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Herbs	-0.07	-0.21	-0.53
Shrubs 0-1m	0.24	0.36	-0.17
Shrubs 1-3m	-0.01	0.23	0.06

Table D4. Axis summary statistics for the Cumberland Plateau ecoregion.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalue	0.31	0.21	0.17
Variance in species data			
% of variance explained	14.20	9.60	7.90
Cumulative % explained	14.20	23.80	31.70
Pearson Correlation, Spp-Env*	0.95	0.99	0.95
Kendall (Rank) Corr., Spp-Env	0.73	0.87	0.81

Table D5. Species scores and raw data totals for the Cumberland Plateau ecoregion.

Species	**Axis 1**	**Axis 2**	**Axis 3**	**Raw Data Totals**
Anguispira mordax	0.41	-0.25	0.38	4
Appalachina sayana	0.23	-0.53	0.28	5
Carychium clappi	0.57	0.45	0.80	79
Carychium exile	0.70	-0.50	-0.64	140
Carychium nannodes	0.86	0.55	-0.31	87
Cochilocopa moreseana	-0.46	0.32	-0.13	20
Collumella simplex	1.22	-3.13	-1.96	4
Discus patulus	-0.70	-1.95	-0.29	43
Euchemotrema fraternum	-0.86	0.50	0.64	6
Euconulus fulvus	-0.52	2.18	-3.59	2
Gastrocopta armifera	0.90	0.98	-1.99	2
Gastrocopta contracta	1.18	-0.98	-0.27	17
Gastrocopta contricaria	0.39	2.85	3.08	1
Gastrodonta interna	-1.20	-1.96	0.57	10
Glyphyalinia cryptomphala	0.98	-0.04	-1.98	4
Glyphyalinia indentata	-0.94	0.82	-0.94	17
Glyphyalinia wheatleyi	1.12	0.82	1.78	30
Guppya sterkii	1.46	0.03	1.36	21
Haplotrema concavum	-0.61	-0.34	1.43	20
Hawaii miniscula	-0.35	1.84	-0.79	15

Table D5. (Continued)

Species	**Axis 1**	**Axis 2**	**Axis 3**	**Raw Data Totals**
Helicodiscus notius	-1.22	-1.10	2.20	1
Inflectarius inflectus	-1.31	-1.39	-0.63	4
Inflectarius rugeli	-0.55	1.03	0.14	6
Mesodon normalis	-0.78	-0.49	0.66	8
Mesodon zaleatus	-1.68	-4.15	-0.80	1
Mesomphix inornatus	-1.69	-0.12	2.01	39
Mesomphix perlaevis	-1.80	3.37	-1.82	2
Neohelix albolabris	-0.99	0.68	-0.96	4
Paravitrea capsella	-1.71	-0.94	0.23	15
Paravitrea placentula	-0.93	3.47	-1.23	3
Patera appressa	0.25	0.64	-1.66	8
Philomycus carolinensis	-2.66	5.37	-3.19	1
Pomatiopsis lipadaria	0.99	0.04	-1.33	3
Punctum minutissimum	0.03	-0.42	-0.13	15
Pupoides albilabris	0.90	0.98	-1.99	1
Stenotrema stenotrema	-1.50	0.23	-1.30	13
Striatura ferrea	1.95	1.28	2.86	4
Striatura meridionalis	1.95	1.28	2.86	4
Strobilops aenea	1.29	0.13	0.58	1
Triodopsis spp.	0.99	0.43	0.68	3
Triodopsis tridentata	-0.89	0.10	0.15	43
Ventridens demissus	-1.09	3.52	-1.21	7
Ventridens gularis	-1.29	0.32	-0.35	34
Ventridens lasmodon	-3.33	2.50	-2.12	4
Ventridens lawae	-1.68	-4.15	-0.80	1
Ventridens ligera	-2.99	0.45	0.84	2
Ventridens theloides	0.17	0.75	0.06	2
Vertigo bollesiana	0.26	-0.86	-0.65	8
Vetigo gouldii	1.58	-0.92	0.44	2
Vertigo parvula	-0.72	0.86	-1.16	7
Xolotrema denotatum	-1.13	-2.59	0.26	2
Zonitoides arboreus	-0.27	-0.10	-1.37	1
Zonitoides elliotti	1.17	2.07	2.97	2

Table D6. Inter-set correlations for the 15 environmental variables collected on the Cumberland Plateau ecoregion.

	Correlations		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Elevation	0.16	0.10	0.10
Slope	0.49	0.26	-0.17
Aspect	-0.06	-0.42	0.59
pH	-0.37	-0.44	0.42
Soil Temperature	-0.47	-0.31	0.43
Soil Moisture	0.53	0.35	-0.18
Duff	0.55	-0.42	-0.13
Cover	0.71	0.07	-0.22
Leaf Litter	-0.11	0.65	0.11
Bare Ground	0.47	0.15	0.27
Rock	0.11	-0.46	-0.16
CWD	-0.15	-0.31	0.09
Herbs	0.59	0.22	0.28
Shrubs 0-1m	0.24	0.36	-0.17
Shrubs 1-3m	-0.01	0.23	0.061

Table D7. Axis summary statistics for the Pine Mountain ecorgeion.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalue	0.54	0.46	0.28
Variance in species data			
% of variance explained	16.20	13.80	8.70
Cumulative % explained	16.20	30.10	38.80
Pearson Correlation, Spp-Env*	0.96	0.95	0.93
Kendall (Rank) Corr., Spp-Env	0.68	0.83	0.71

Table D8. Species scores and raw data totals for the Pine Mountain ecoregion.

Species	**Axis 1**	**Axis 2**	**Axis 3**	**Raw Data Totals**
Anguispira mordax	-1.23	-0.13	-0.20	3
Appalachina sayana	0.08	-0.21	0.31	5
Carychium clappi	1.59	-0.89	0.30	51
Carychium exile	0.55	1.54	-2.07	13
Carychium nannodes	0.69	0.34	-1.08	12
Cochilocopa moreseana	0.36	-0.05	-0.64	7
Discus patulus	0.43	3.10	1.95	6

Table D8. (Continued)

Species	**Axis 1**	**Axis 2**	**Axis 3**	**Raw Data Totals**
Euchemotrema fraternum	-0.35	0.62	0.63	4
Gastrocopta contracta	2.24	-1.97	1.20	1
Gastrodonta interna	-0.94	-0.21	0.97	2
Glyphyalinia indentata	-0.32	0.68	-1.62	11
Glyphyalinia wheatleyi	-0.66	-0.30	-1.07	17
Haplotrema concavum	0.30	-0.58	-1.08	4
Hawaii miniscula	-0.22	-0.14	-2.25	2
Inflectarius rugeli	-0.77	-0.47	-0.91	6
Mesodon normalis	-0.48	0.41	1.65	10
Mesomphix cupreus	-1.27	0.12	1.50	2
Mesomphix inornatus	-1.05	-0.47	0.59	11
Palifera dorsalis	0.77	4.59	1.60	1
Paravitrea capsella	-1.37	-0.91	-2.76	4
Patera appressa	1.10	2.24	-0.03	9
Philomycus carolinensis	0.77	4.59	1.60	1
Pomatiopsis lipadaria	1.92	-0.85	0.06	1
Punctum minutissimum	0.03	-0.03	1.04	7
Stenotrema stenotrema	1.13	-0.88	0.57	4
Triodopsis tridentata	-0.46	-0.68	-0.48	6
Ventridens demissus	-1.15	-0.01	0.16	19
Ventridens gularis	-0.88	-0.31	0.32	36
Ventridens ligera	0.85	1.45	-0.16	2
Ventridens lasmodon	-0.67	-0.84	0.74	14
Vertigo bollesiana	-0.66	0.95	1.31	9
Xolotrema denotatum	-1.52	-0.42	0.07	2
Zonitoides arboreus	0.42	2.14	-0.06	2

Table D9. Inter-set correlations for the 15 environmental variables collected at the Pine Mountain ecoregion.

	Correlations		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Elevation	-0.52	0.03	0.39
Slope	-0.07	-0.41	0.19
Aspect	-0.18	-0.19	-0.43
pH	0.09	-0.53	0.23
Soil Temperature	-0.19	0.01	0.15
Soil Moisture	-0.29	-0.26	-0.16
Duff	-0.21	0.07	-0.08

Table D9. (Continued)

Variable	Correlations		
	Axis 1	**Axis 2**	**Axis 3**
Cover	-0.15	0.27	-0.06
Leaf Litter	-0.30	-0.27	-0.20
Bare Ground	-0.40	-0.18	0.10
Rock	0.23	0.28	0.49
CWD	0.27	0.10	-0.34
Herbs	-0.13	-0.29	0.24
Shrubs 0-1m	-0.34	0.08	0.07
Shrubs 1-3m	0.02	-0.07	0.20

APPENDIX E: INDICATOR SPECIES ANALYSIS TABLES FOR EACH ECOREGION SAMPLED.

Table E1. Percent of perfect indication (% IV) based on combining values of relative abundance and relative frequency for all ecoregions studied. Avg = the average number of individuals, Max = the maximum number of individuals, Group (% IV) = group to which each species was indicative (OG = old-growth, SG = second-growth), and Std. Dev = standard deviation. Statistically significant species based on the Monte Carlo permutations test are bolded and highlighted in gray.

			Group (% IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Anguispira alternata	13	20		20	4.43	0.21
Anguispira kochi	13	16	16		4.40	0.73
Anguispira mordax	7	12		12	3.37	0.42
Appalachina sayana	23	30	30		5.02	0.33
Carychium clappi	**37**	**51**	**51**		**4.72**	**0.04**
Carychium exile	**39**	**65**	**65**		**4.96**	**<0.001**
Carychium nannodes	**34**	**53**	**53**		**5.12**	**0.01**
Catinella oklahomarum	10	14	14		4.03	0.37
Cochilocopa moreseana	**31**	**55**	**55**		**5.09**	**0.001**
Collumella simplex	**18**	**35**	**35**		**4.38**	**<0.001**
Discus patulus	26	39	39		5.34	0.10
Euchemotrema fraternum	21	34	34		5.02	0.08
Euconulus fulvus	12	12	12		4.32	0.95
Gastrocopta armifera	**16**	**29**	**29**		**4.76**	**0.03**
Gastrocopta contracta	**21**	**38**	**38**		**5.18**	**0.01**
Gastrocopta contricaria	2	3	3		0.05	1.00
Gastrocopta pentodon	**14**	**26**	**26**		**4.43**	**0.03**
Gastrocopta procera	**17**	**33**	**33**		**3.98**	**0.001**
Gastrodonta interna	22	36	36		5.30	0.10
Glyphyalinia cryptomphala	5	9		9	2.91	0.23
Glyphyalinia indentata	**28**	**46**	**46**		**4.85**	**0.01**
Glyphyalinia wheatleyi	29	38	38		5.42	0.28
Guppya sterkii	**17**	**31**	**31**		**4.78**	**0.03**
Haplotrema concavum	**28**	**48**	**48**		**5.09**	**<0.01**
Hawaii miniscula	**21**	**35**	**35**		**4.86**	**0.04**
Helicodiscus notius	11	18	18		4.14	0.27
Inflectarius inflectus	13	16		16	4.36	0.76
Inflectarius rugeli	21	21	21	21	4.67	1.00
Mesodon elevatus	14	15	15		4.44	0.96
Mesodon thyroidus	11	15	15		4.16	0.44
Mesodon normalis	10	12		12	4.23	0.72
Mesodon zaleatus	9	14	14		3.77	0.25
Mesomphix cupreus	**11**	**21**	**21**		**3.82**	**0.04**
Mesomphix inornatus	27	30		30	4.8	0.61

Table E1. (Continued)

			Group (% IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Mesomphix perlaevis	**18**	**32**	**32**		**4.47**	**0.02**
Mesomphix vulgatus	3	7	7		2.50	0.49
Neohelix albolabris	12	13	13		4.43	0.89
Palifera dorsalis	2	3	3		0.05	1.00
Paravitrea capsella	17	24	24		4.52	0.25
Paravitrea placentula	5	10	10		2.37	0.23
Patera appressa	**23**	**42**	**42**		**4.65**	**<0.01**
Philomycus carolinensis	3	7	7		2.50	0.49
Pomatiopsis lipadaria	11	17	17		4.09	0.30
Punctum blandianum	5	10	10		2.73	0.23
Punctum minutissimum	23	28	28		4.86	0.46
Pupoides albilabris	8	9	9		3.77	0.91
Stenotrema angellum	10	16		16	3.92	0.29
Stenotrema barbatum	8	8	8	8	3.92	1.00
Stenotrema stenotrema	13	15	15		4.51	0.83
Striatura ferrea	**13**	**27**	**27**		**3.79**	**<0.01**
Striatura meridionalis	14	20	20		4.50	0.37
Strobilops aenea	12	18	18		4.31	0.34
Strobilops labyrinthica	10	12	12		4.08	0.72
Triodopsis sp.	5	10	10		2.36	0.23
Triodopsis tridentata	21	31		31	5.17	0.16
Vallonia exentrica	**12**	**23**	**23**		**3.41**	**0.01**
Ventridens demissus	12	18	18		4.35	0.28
Ventridens gularis	18	20	20		4.97	0.71
Ventridens intertextus	10	19		19	3.90	0.10
Ventridens ligera	13	16	16		4.57	0.65
Ventridens lasmodon	11	19		19	4.11	0.14
Ventridens lawae	2	3	3		0.05	1.00
Ventridens theloides	3	7	7		2.50	0.49
Vertigo bollesiana	2	3	3		0.05	1.00
Vertigo parvula	9	16	16		4.07	0.24
Vertigo gouldii	11	16	16		4.32	0.40
Vertigo tridentata	14	17	17		4.54	0.70
Xolotrema denotatum	12	14	14		4.22	0.74
Zonitoides arboreus	15	17	17		4.54	0.79
Zonitoides elliotti	3	7	7		2.50	0.49

Table E2. Percent of perfect indication (% IV) based on combining values of relative abundance and relative frequency for the Inner Bluegrass ecoregion. Avg = the average number of individuals, Max = the maximum number of individuals, Group (%IV) = group to which each species was indicative (OG = old-growth, SG = second-growth), and Std. Dev = standard deviation. Statistically significant species based on the Monte Carlo permutations test are bolded and highlighted in gray.

			Group (% IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Anguispira alternata	39	61		61	8.47	0.07
Anguispira kochi	40	47	47		6.68	0.55
Appalachina sayana	43	48	48		6.43	0.65
Carychium clappi	**50**	**60**	**60**		**2.47**	**0.01**
Carychium exile	**50**	**61**	**61**		**2.66**	**<0.01**
Carychium nannodes	**50**	**60**	**60**		**2.27**	**<0.01**
Catinella oklahomarum	29	43	43		9.1	0.26
Cochilocopa moreseana	**45**	**70**	**70**		**6.61**	**0.01**
Collumella simplex	**47**	**86**	**86**		**7.61**	**<0.001**
Discus patulus	40	62	62		7.55	0.06
Euchemotrema fraternum	43	53	53		6.09	0.41
Euconulus fulvus	38	48		48	7.13	0.41
Gastrocopta armifera	**48**	**85**	**85**		**7.47**	**<0.001**
Gastrocopta contracta	**48**	**87**	**87**		**8.25**	**<0.001**
Gastrocopta pentodon	**43**	**68**	**68**		**8.59**	**0.05**
Gastrocopta procera	**50**	**100**	**100**		**9.18**	**<0.001**
Gastrodonta interna	**48**	**88**	**88**		**7.88**	**<0.001**
Glyphyalinia indentata	**42**	**64**	**64**		**7.18**	**0.04**
Glyphyalinia wheatleyi	**41**	**72**	**72**		**8.24**	**<0.01**
Guppya sterkii	**41**	**69**	**69**		**7.89**	**0.02**
Haplotrema concavum	**42**	**73**	**73**		**8.15**	**<0.01**
Hawaii miniscula	**42**	**65**	**65**		**7.18**	**0.03**
Helicodiscus notius	33	41	41		7.81	0.48
Inflectarius inflectus	35	44		44	7.8	0.56
Inflectarius rugeli	36	47	47		7.63	0.45
Mesodon elevatus	43	45	45		5.74	0.92
Mesodon thyroidus	31	45	45		8.74	0.28
Mesodon zaleatus	27	39	39		9.21	0.34
Mesomphix cupreus	**35**	**70**	**70**		**8.99**	**<0.01**
Mesomphix inornatus	38	47		47	7.54	0.42
Mesomphix perlaevis	41	52	52		6.44	0.31
Neohelix albolabris	30	37		37	8.8	0.64
Paravitrea capsella	31	43	43		8.61	0.40
Patera appressa	41	51	51		6.54	0.39

Table E2. (Continued)

			Group (% IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Pomatiopsis lipadaria	28	36	36		8.64	0.59
Punctum minutissimum	35	38		38	8.04	0.84
Pupoides albilabris	28	32		32	8.51	0.88
Stenotrema angellum	30	48		48	8.4	0.16
Stenotrema barbatum	25	25	25	25	8.91	1.00
Stenotrema stenotrema	23	25		25	8.96	0.96
Striatura meridionalis	40	51	51		6.89	0.37
Strobilops aenea	34	46	46		8.14	0.33
Strobilops labyrinthica	30	37	37		8.44	0.64
Triodopsis tridentata	25	45		45	9.46	0.16
Vallonia exentrica	**35**	**70**	**70**		**8.71**	**<0.01**
Ventridens intertextus	**31**	**56**		**56**	**9.07**	**0.04**
Ventridens ligera	33	37	37		7.75	0.87
Vertigo tridentata	43	51	51		6.07	0.49
Xolotrema denotatum	31	42		42	8.78	0.44
Zonitoides arboreus	38	46		46	7.1	0.54

Table E3. Percent of perfect indication (% IV) based on combining values of relative abundance and relative frequency for the Cumberland Plateau ecoregion. Avg = the average number of individuals, Max = the maximum number of individuals, Group (%IV) = group to which each species was indicative (OG = old-growth, SG = second-growth), and Std. Dev = standard deviation. Statistically significant species based on the Monte Carlo permutations test are bolded and highlighted in gray.

			Group (% IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Anguispira mordax	10	10	10	10	8.86	1.00
Appalachina sayana	17	32	32	2	8.09	0.30
Carychium clappi	**37**	**65**	**65**	**9**	**9.64**	**0.04**
Carychium exile	**47**	**90**	**90**	**3**	**10.08**	**<0.001**
Carychium nannodes	**39**	**75**	**75**	**2**	**11.27**	**<0.01**
Cochilocopa moreseana	**31**	**56**	**56**	**6**	**9.2**	**<0.01**
Collumella simplex	5	10	10	0	0.14	1.00
Discus patulus	37	46	46	28	9.61	0.59
Euchemotrema fraternum	15	15	15	15	9.38	1.00
Euconulus fulvus	5	10	10	0	0.14	1.00
Gastrocopta armifera	5	10	10	0	0.14	1.00
Gastrocopta contracta	19	38	38	1	8.89	0.08
Gastrocopta contricaria	5	10	10	0	0.14	1.00

Table E3. (Continued)

			Group (% IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Gastrodonta interna	20	20	20	20	9.1	1.00
Glyphyalinia cryptomphala	10	20	20	0	6.25	0.47
Glyphyalinia indentata	**31**	**56**	**56**	**6**	**9.02**	**0.03**
Glyphyalinia wheatleyi	28	54	54	2	10.65	0.08
Guppya sterkii	19	38	38	0	9.51	0.14
Haplotrema concavum	35	39	39	31	8.19	0.83
Hawaii miniscula	**28**	**56**	**56**	**1**	**9.11**	**0.02**
Helicodiscus notius	5	10	0	10	0.14	1.00
Inflectarius inflectus	10	20	20	0	7.5	0.48
Inflectarius rugeli	22	42	42	2	9.11	0.13
Mesodon normalis	15	19	11	19	9.31	0.77
Mesodon zaleatus	5	10	10	0	0.14	1.00
Mesomphix inornatus	39	41	37	41	7.33	0.86
Mesomphix perlaevis	10	20	20	0	7.49	0.47
Neohelix albolabris	20	40	40	0	8.91	0.08
Paravitrea capsella	18	24	12	24	8.76	0.68
Paravitrea placentula	15	30	30	0	6.82	0.21
Patera appressa	**25**	**50**	**50**	**0**	**8.82**	**0.03**
Philomycus carolinensis	5	10	10	0	0.14	1.00
Pomatiopsis lipadaria	5	7	7	3	6.66	1.00
Punctum minutissimum	**35**	**69**	**69**	**1**	**9.54**	**<0.01**
Pupoides albilabris	5	10	10	0	0.14	1.00
Stenotrema stenotrema	22	38	38	5	9.07	0.18
Striatura ferrea	2	4	14	0	0.14	1.00
Striatura meridionalis	5	10	10	0	0.14	1.00
Strobilops aenea	5	10	10	0	0.14	1.00
Triodopsis spp.	15	30	30	0	6.81	0.21
Triodopsis tridentata	37	54	54	20	9.46	0.20
Ventridens demissus	15	30	30	0	7.44	0.20
Ventridens gularis	27	42	42	12	9.65	0.25
Ventridens lasmodon	8	10	5	10	7.07	1.00
Ventridens lawae	5	10	10	0	0.14	1.00
Ventridens ligera	10	20	0	20	7.49	0.47
Ventridens theloides	10	20	20	0	7.48	0.46
Vertigo bollesiana	23	44	44	1	8.72	0.11
Vetigo gouldii	10	20	20	0	7.49	0.47
Vertigo parvula	**30**	**60**	**60**	**0**	**8.99**	**0.01**
Xolotrema denotatum	5	5	5	5	7.48	1.00
Zonitoides arboreus	5	10	10	0	0.14	1.00

Table E3. (Continued)

Species	Avg	Max	Group (% IV) OG	SG	Std. Dev	p*value
Zonitoides elliotti	10	20	20	0	7.49	0.47

Table E4. Percent of perfect indication (% IV) based on combining values of relative abundance and relative frequency for the Pine Mountain ecoregion. Avg = the average number of individuals, Max = the maximum number of individuals, Group (%IV) = group to which each species was indicative (OG = old-growth, SG = second-growth), and Std. Dev = standard deviation. Statistically significant species based on the Monte Carlo permutations test are bolded and highlighted in gray.

			Group (%IV)			
Species	**Avg**	**Max**	**OG**	**SG**	**Std. Dev**	**p*value**
Anguispira mordax	15	30	0	30	6.84	0.21
Appalachina sayana	13	18	18	8	8.03	1.00
Carychium clappi	25	31	31	20	11.14	0.71
Carychium exile	**35**	**70**	**70**	**0**	**10**	**<0.01**
Carychium nannodes	21	37	37	5	9.18	0.23
Cochilocopa moreseana	17	29	29	6	8.74	0.45
Discus patulus	9	17	17	2	7.12	0.46
Euchemotrema fraternum	10	10	10	10	8.98	1.00
Gastrocopta contracta	5	10	0	10	0.14	1.00
Gastrodonta interna	10	20	0	20	7.49	0.47
Glyphyalinia indentata	18	33	33	4	9.4	0.31
Glyphyalinia wheatleyi	26	39	14	39	8.88	0.37
Haplotrema concavum	15	30	30	0	7.01	0.20
Hawaii miniscula	5	5	5	5	7.48	1.00
Inflectarius rugeli	13	15	10	15	8.29	1.00
Mesodon normalis	15	18	12	18	8.98	0.96
Mesomphix cupreus	10	20	0	20	7.49	0.47
Mesomphix inornatus	13	19	7	19	8.69	0.78
Palifera dorsalis	5	10	10	0	0.14	1.00
Paravitrea capsella	8	10	10	5	7.13	1.00
Patera appressa	**25**	**50**	**50**	**0**	**8.58**	**0.03**
Philomycus carolinensis	5	10	10	0	0.14	1.00
Pomatiopsis lipadaria	5	10	10	0	0.14	1.00
Punctum minutissimum	15	17	17	13	9.09	1.00
Stenotrema stenotrema	8	10	5	10	7.11	1.00
Triodopsis tridentata	12	20	3	20	8.55	0.58

Table E4. (Continued)

Species	**Avg**	**Max**	**Group (% IV)** **OG**	 **SG**	**Std. Dev**	**p*value**
Ventridens demissus	25	29	29	21	9.69	0.80
Ventridens gularis	35	51	18	51	9.58	0.23
Ventridens ligera	10	20	20	0	7.49	0.47
Ventridens lasmodon	26	47	4	47	9.22	0.10
Vertigo bollesiana	18	27	10	27	9.53	0.72
Xolotrema denotatum	10	20	20	0	7.5	0.48
Zonitoides arboreus	10	20	20	0	7.49	0.47

APPENDIX F: STUDY SITE MAPS

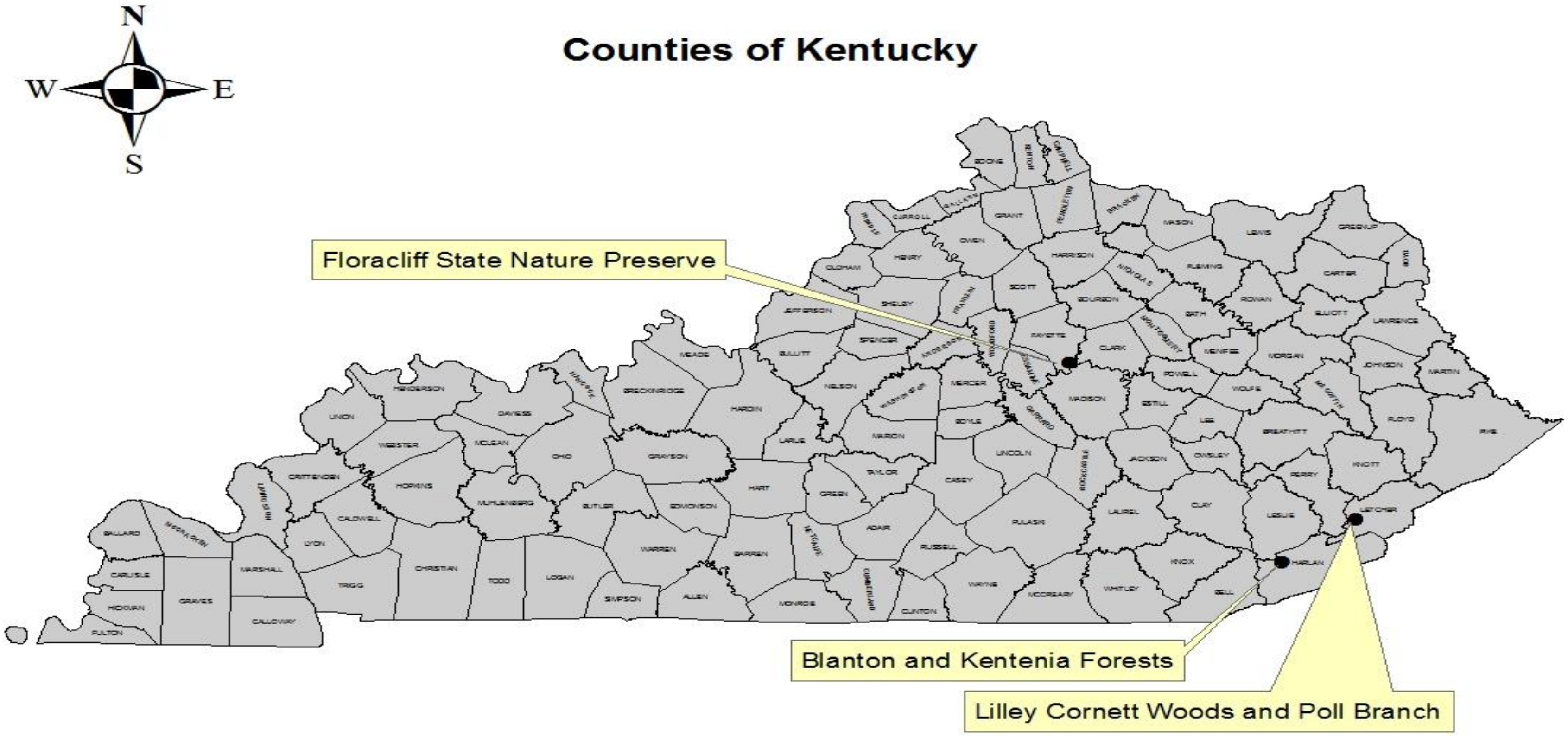

Figure F1. Map showing the counties of Kentucky. Study sites are highlighted by callouts.

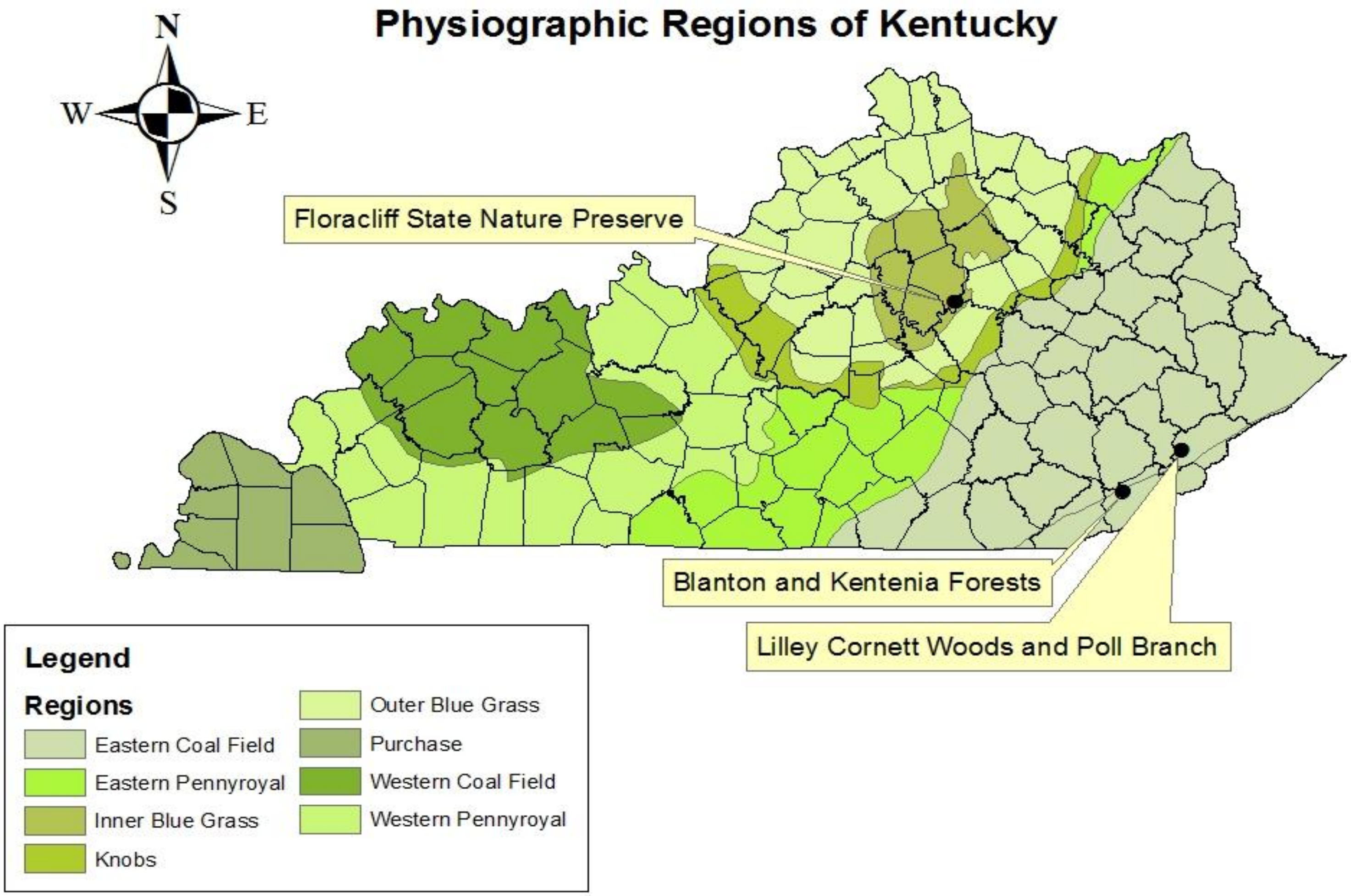

Figure F2. Map showing the Physiographic regions of Kentucky. Study sites are highlighted by callouts.

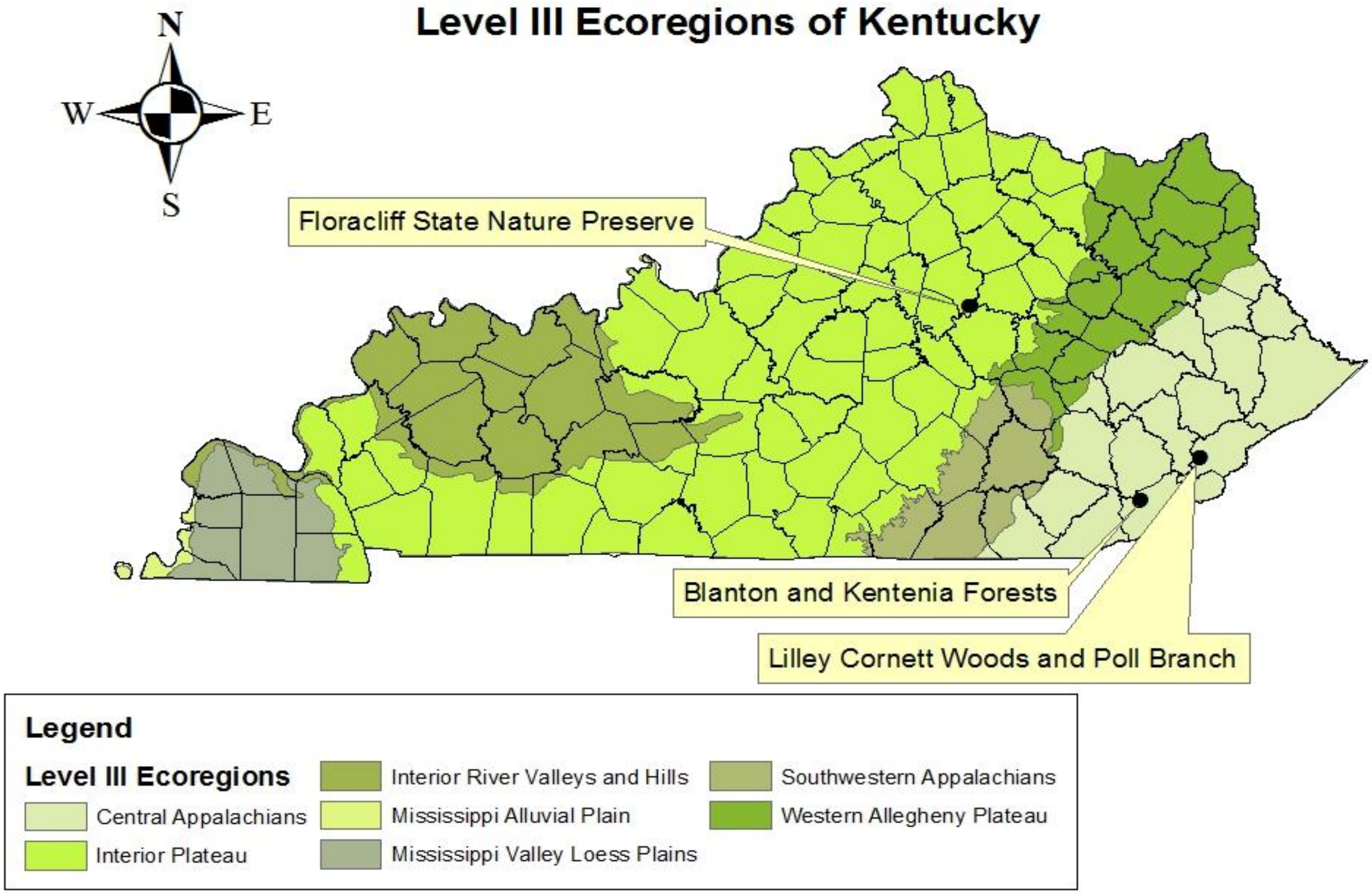

Figure F3. Map showing the Level III Ecoregions of Kentucky. Study sites are highlighted by callouts.

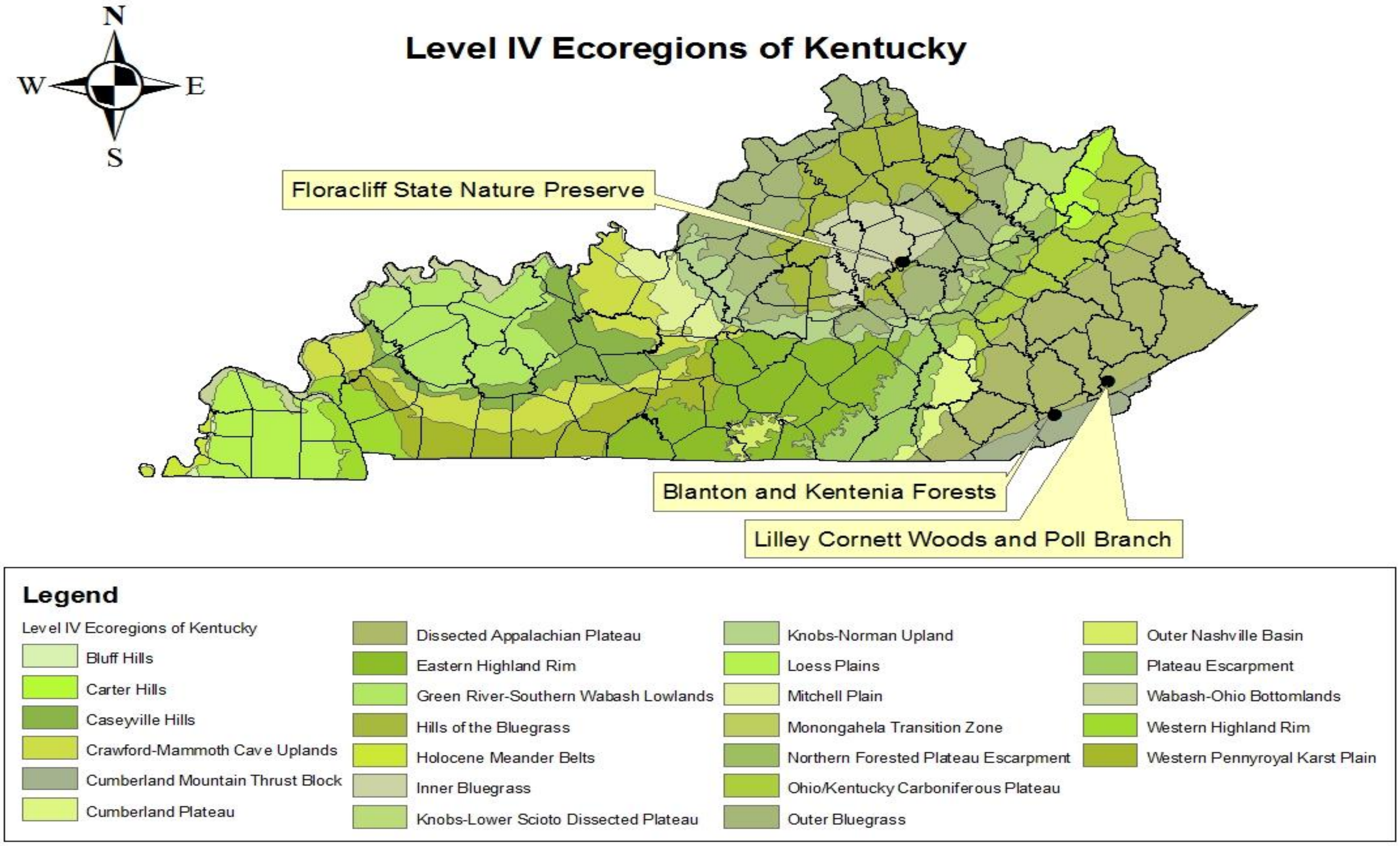

Figure F4. Map showing the Level IV Ecoregions of Kentucky. Study sites are highlighted by callouts.

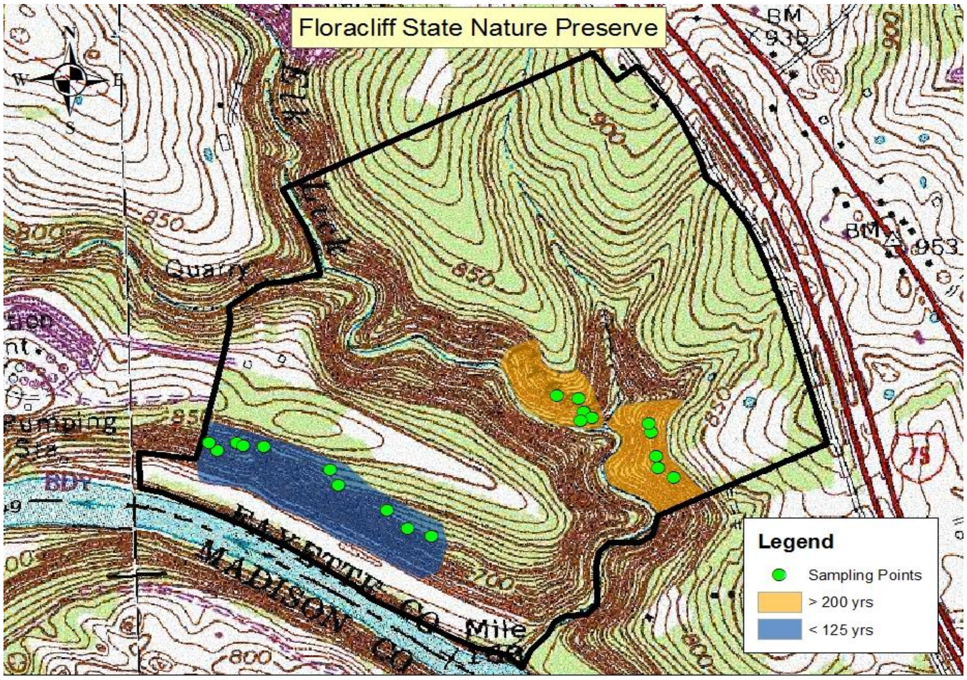

Figure F5. Map showing the boundaries of Floracliff State Nature Preserve (heavy black line). The orange and blue areas represent the different age classes present. The green dots represent sampling points.

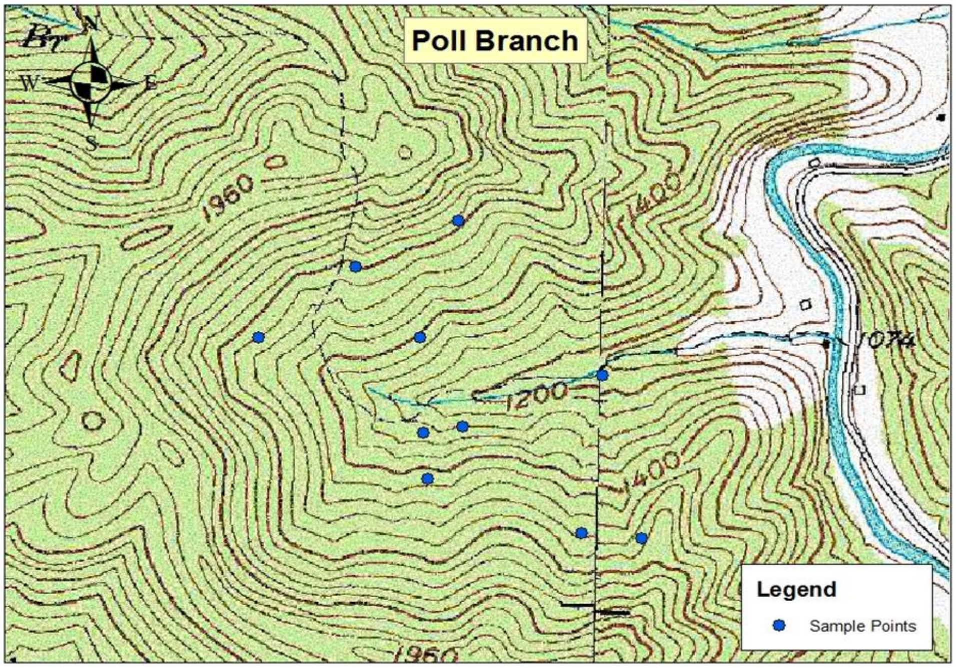

Figure F6. Map showing Poll Branch located just beyond the boundaries of Lilley Cornett Woods. Blue dots represent sampling points.

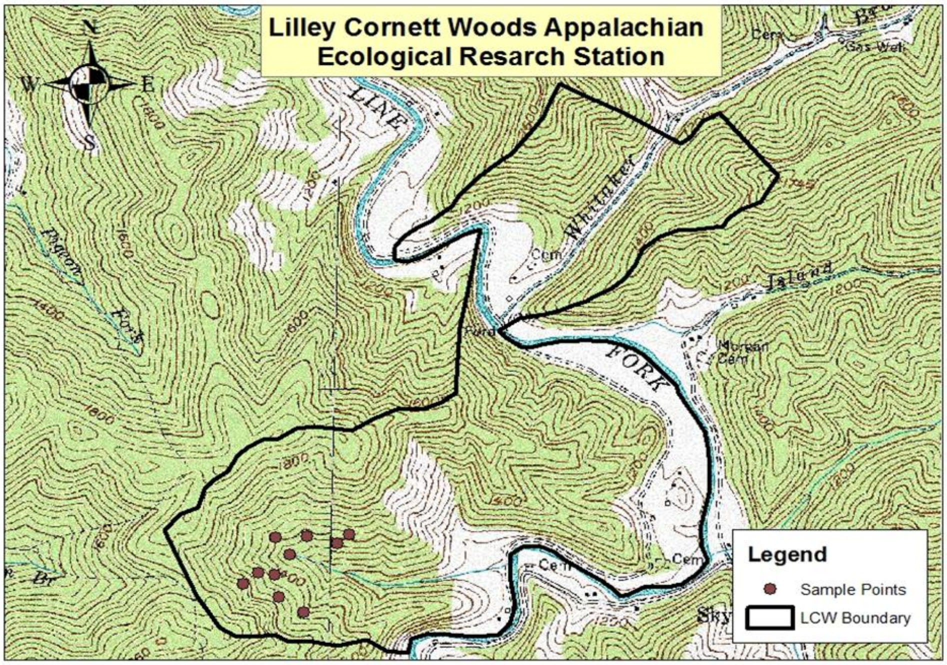

Figure F7. Map showing the boundaries of Lilley Cornett Woods Appalachian Ecological Research Station (heavy dark line). Maroon dots represent sampling points.

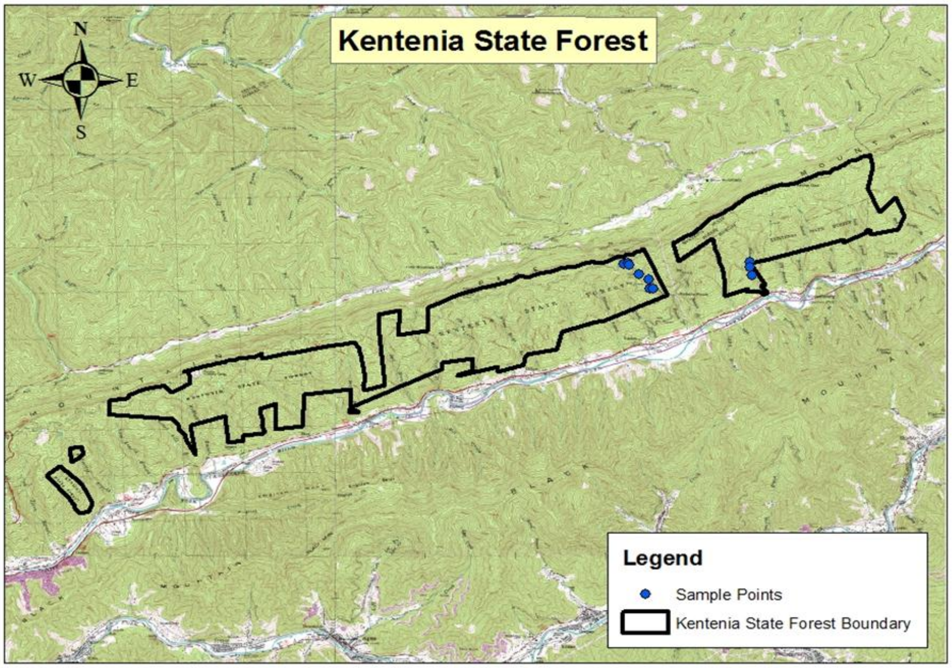

Figure F8. Map showing the boundaries of Kentenia State Forest (heavy dark line). Blue dots represent sampling points.

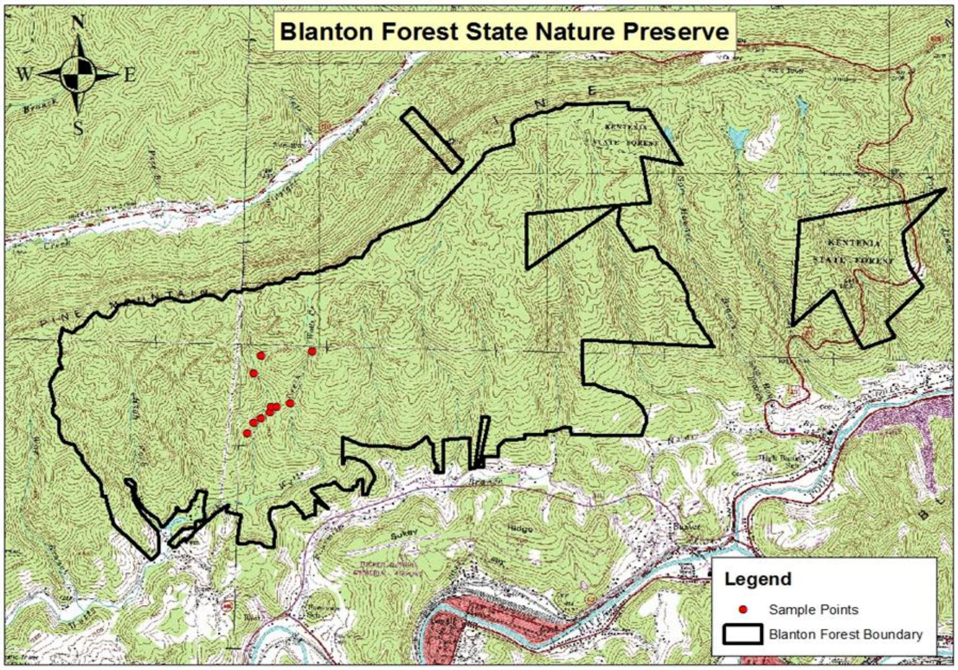

Figure F9. Map showing the boundaries of Blanton Forest State Nature Preserve (heavy dark line). Red dots on the map represent sampling points.

APPENDIX G: DESCRIPTIVE BOX PLOTS FOR HABITAT VARIABLES COLLECTED DURING THE STUDY.

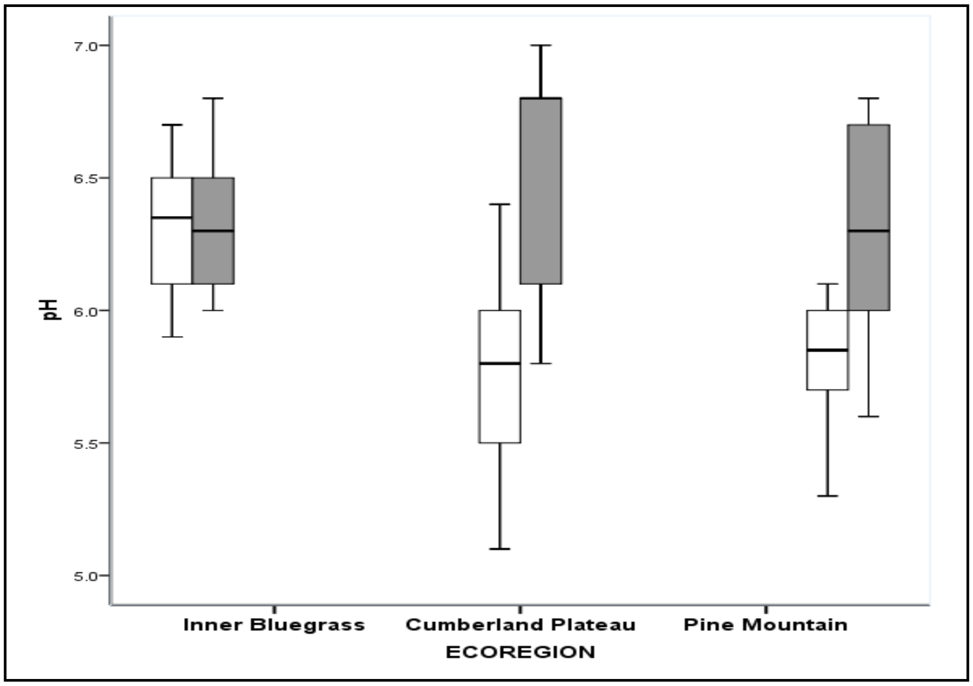

Figure G1. Soil pH for each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

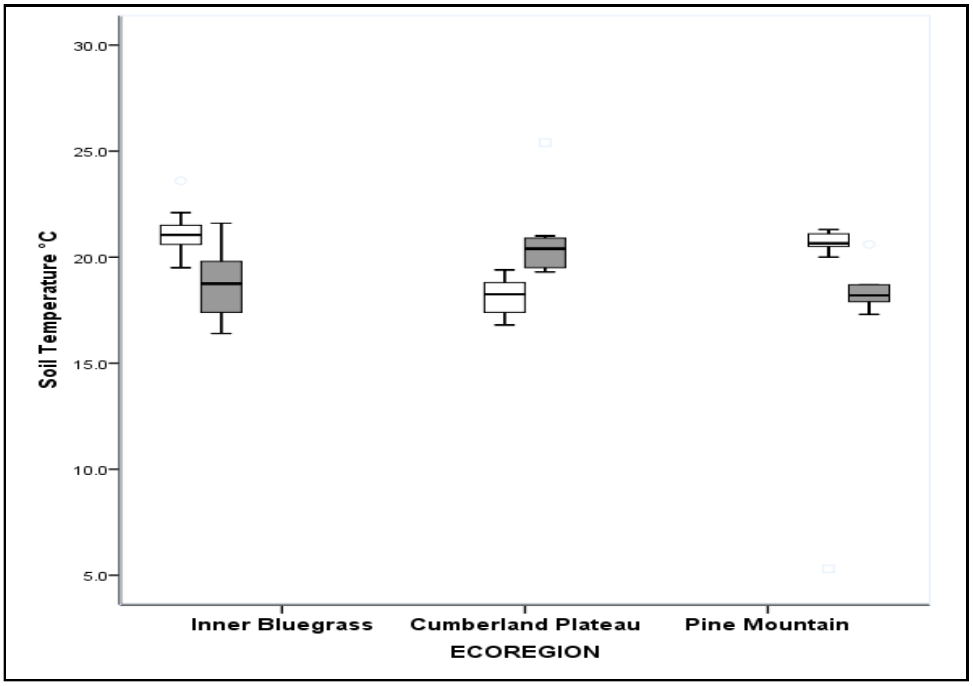

Figure G2**.** Soil temperature °C for each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

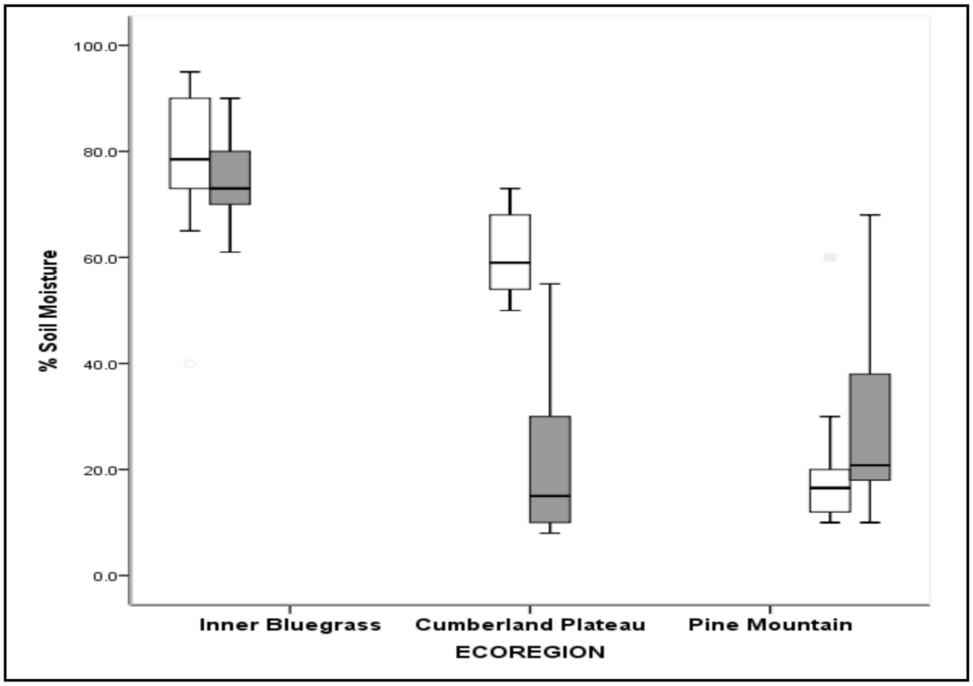

Figure G3. Percent soil moisture for each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

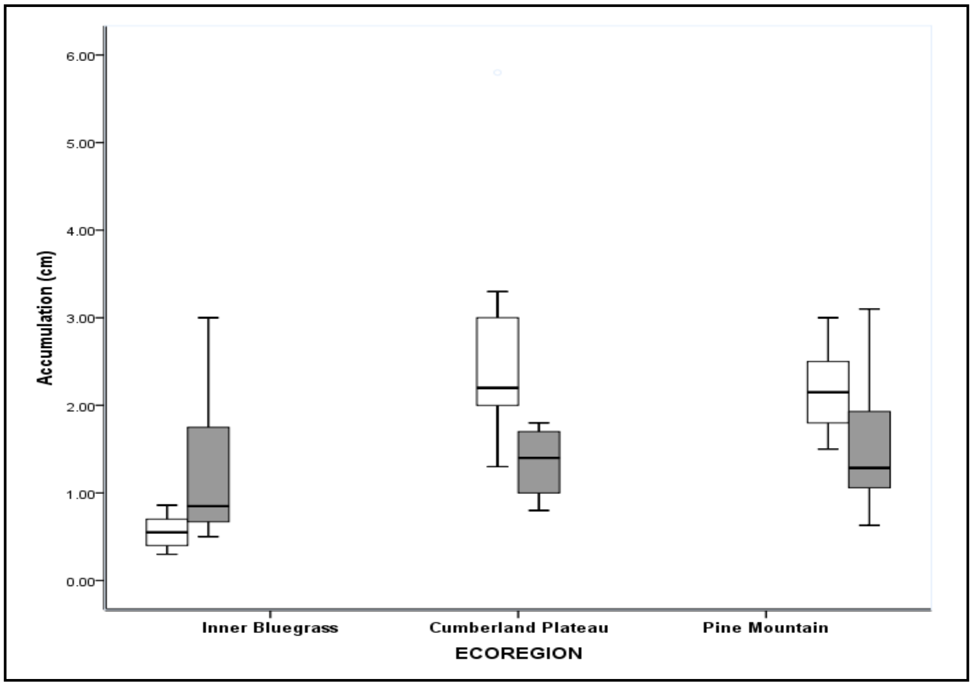

Figure G4. Duff accumulations (cm) for each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

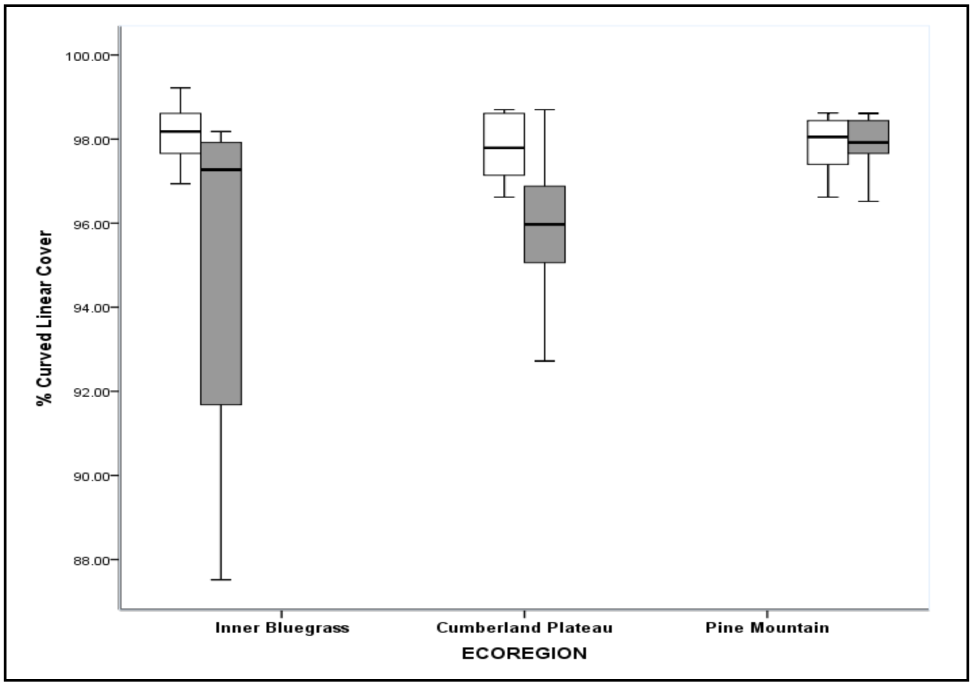

Figure G5. Percent curved linear cover for each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

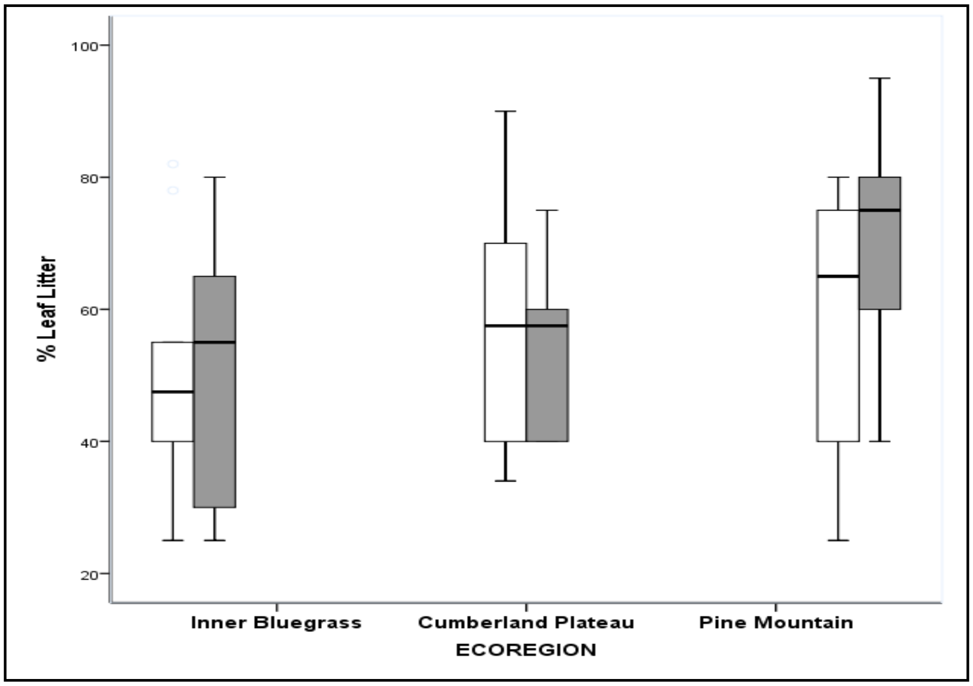

Figure G6. Percent leaf litter at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

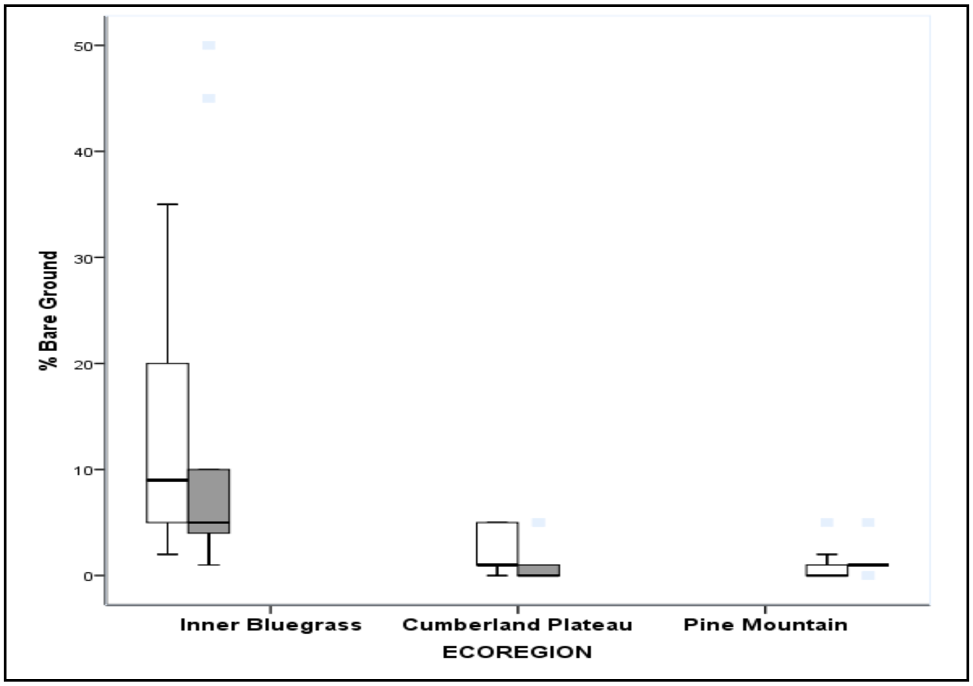

Figure G7. Percent bare ground at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

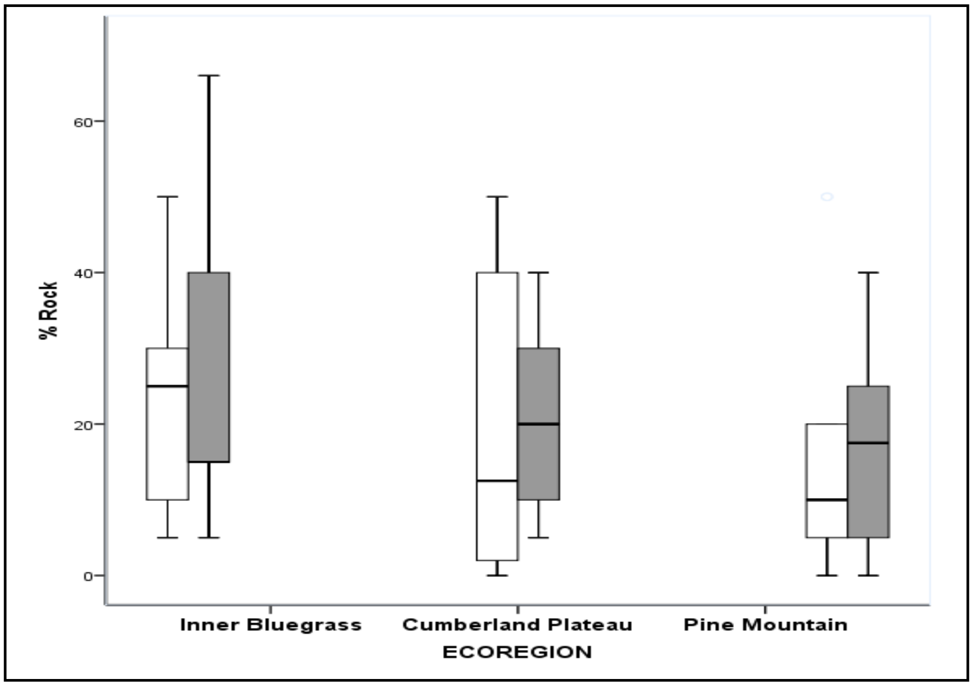

Figure G8. Percent rock at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

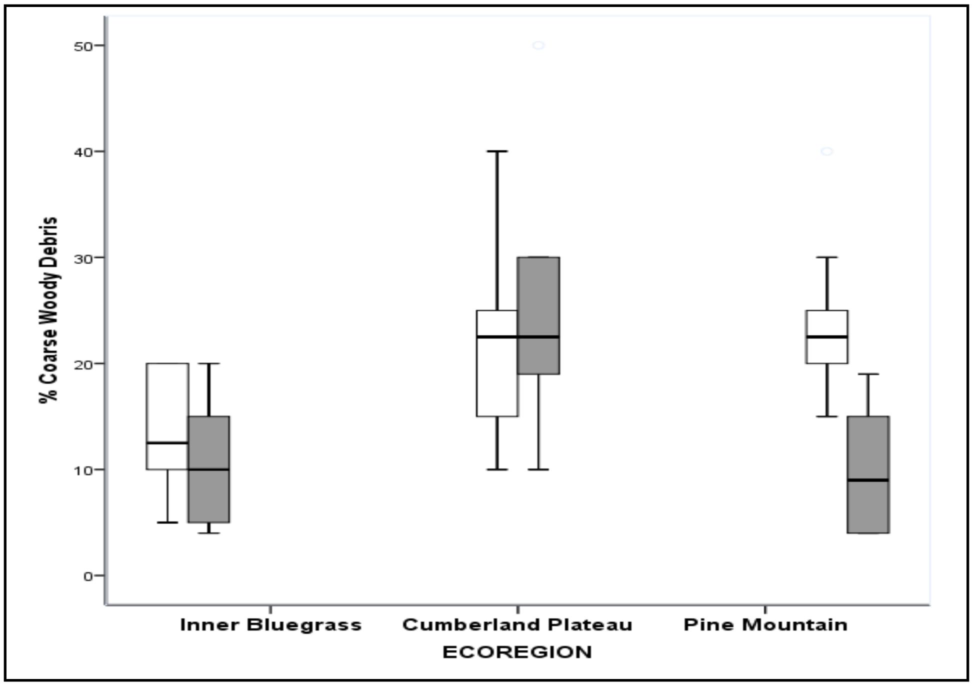

Figure G9. Percent coarse woody debris at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

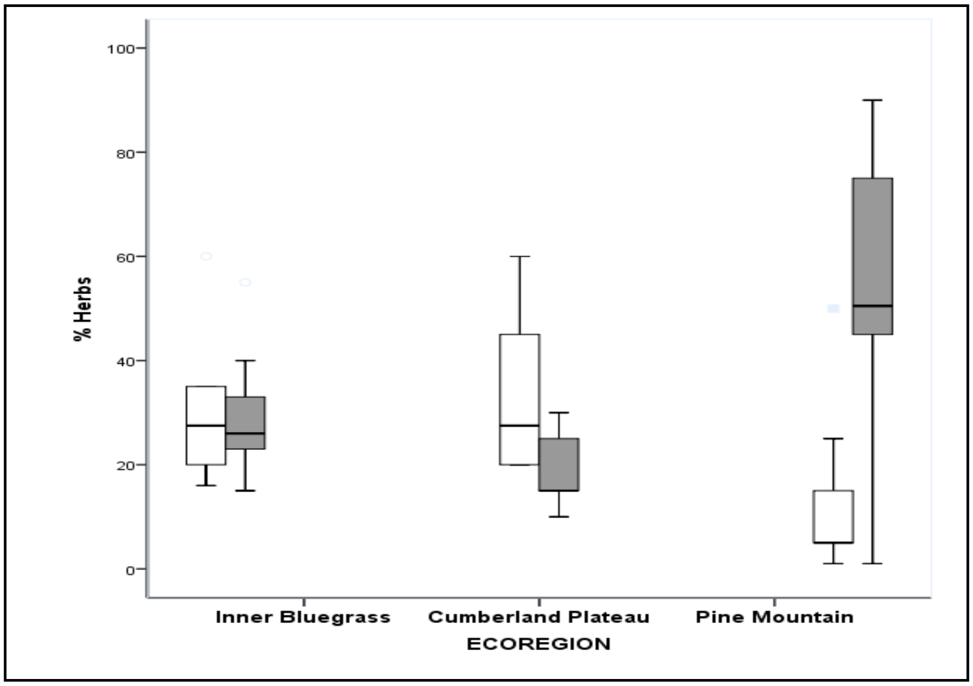

Figure G10. Percent herbaceous cover at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

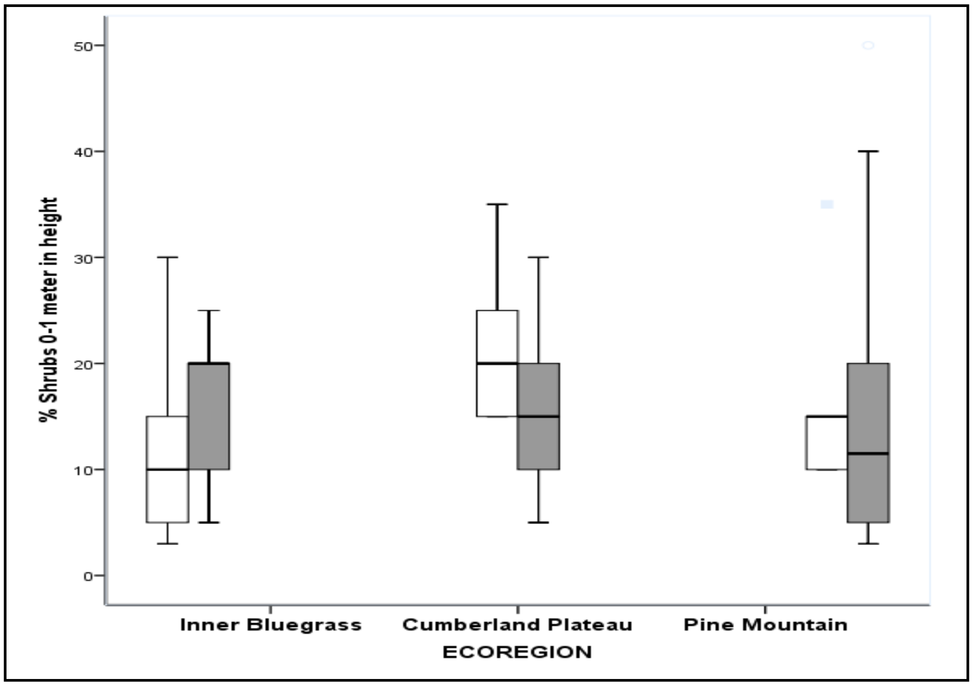

Figure G11. Percent shrubs 0-1 meters in height at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

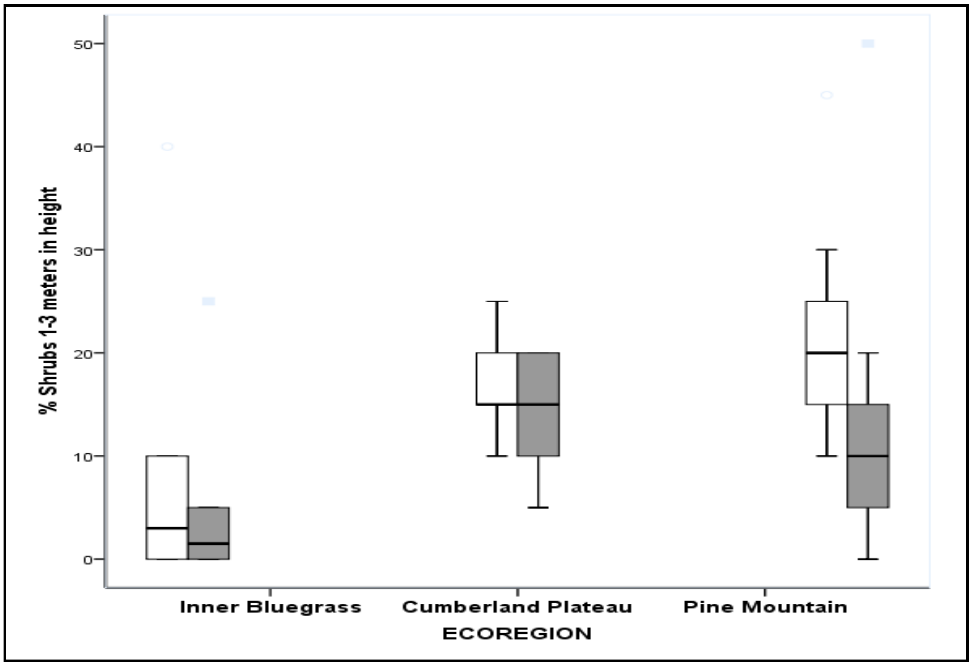

Figure G12. Percent shrubs 1-3 meters in height at each of the study areas. White bars represent old-growth sites and gray bars represent second-growth sites. Black, center bars represent the median of the data set. Bars themselves represent the middle 50% of the data and quartiles extended from boxes represent minimum and maximum data values.

APPENDIX H: RAREFACTION CURVES FOR EACH ECOREGION.

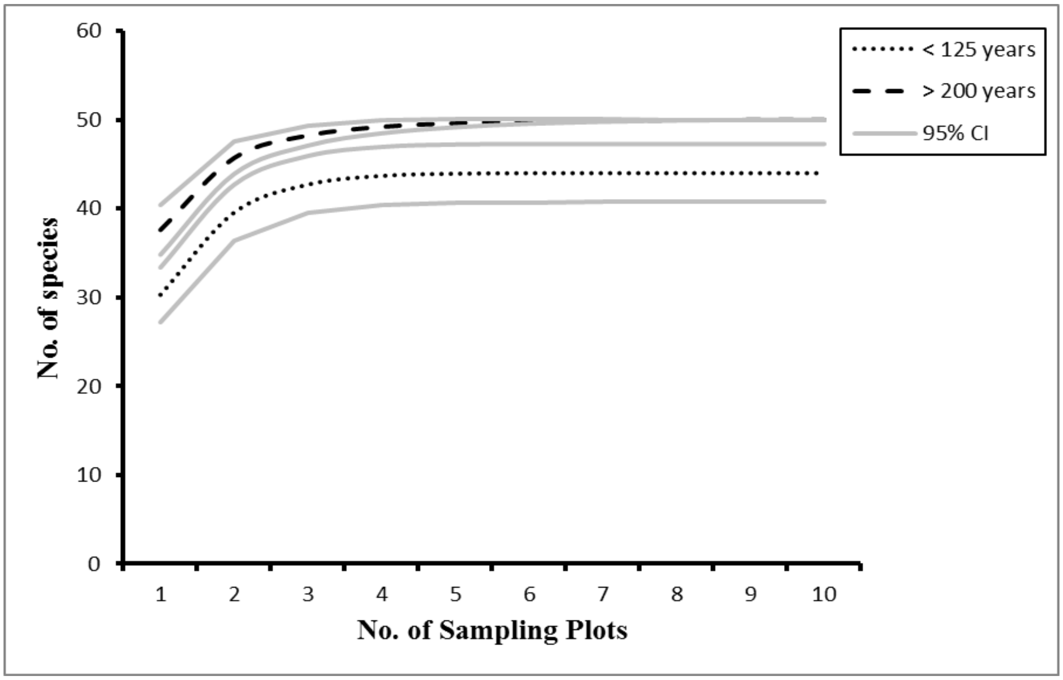

Figure H1. Rarefaction curves for the different disturbance regimes found in the Inner Bluegrass ecoregion. Gray lines represent 95% confidence intervals (CI).

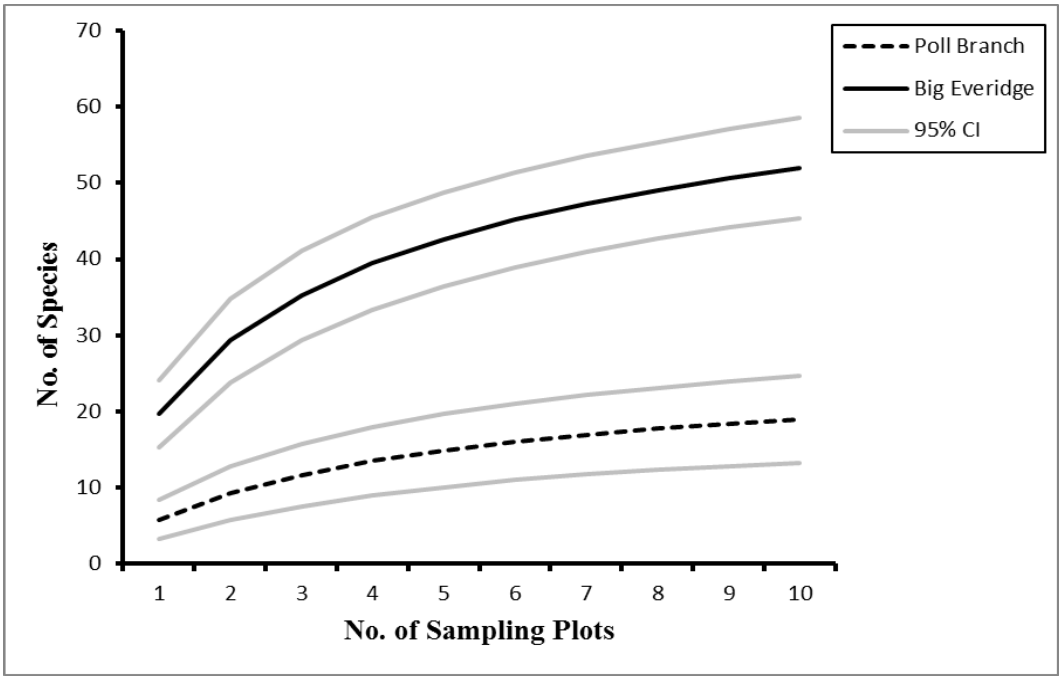

Figure H2. Rarefaction curves for the different disturbance regimes found in the Cumberland Plateau ecoregion. Gray lines represent 95% confidence intervals (CI).

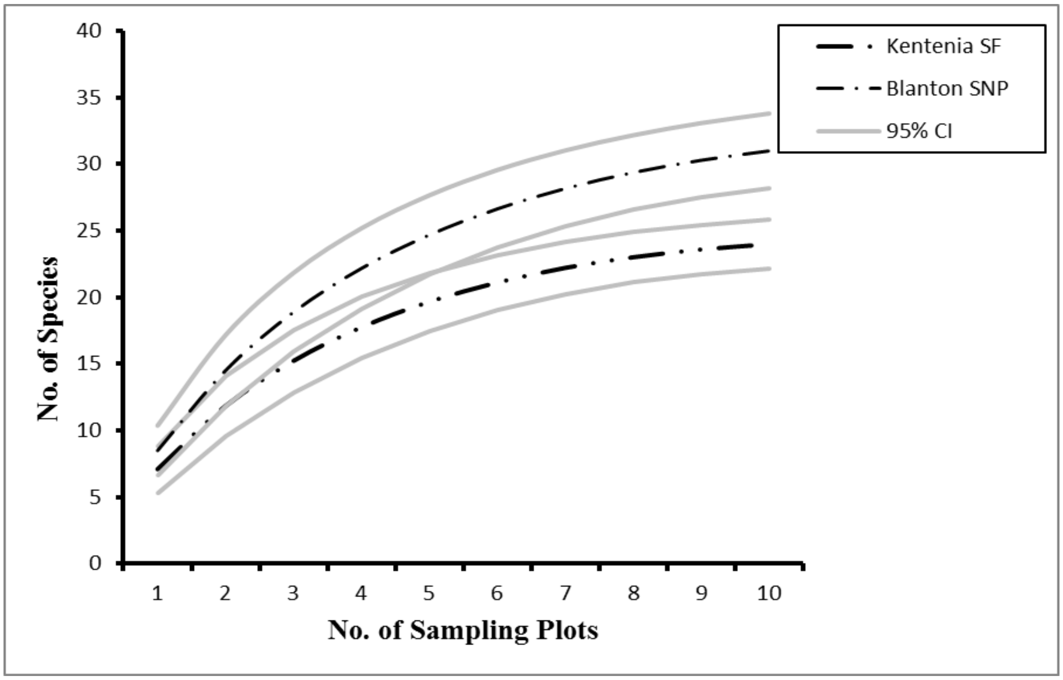

Figure H3. Rarefaction curves for the different disturbance regimes found in the Pine Mountain ecoregion. Gray lines represent 95% confidence intervals (CI).

APPENDIX 1: NON-METRIC MULTIDIMENSIONAL SCALING PLOTS FOR EACH ECOREGION STUDIED.

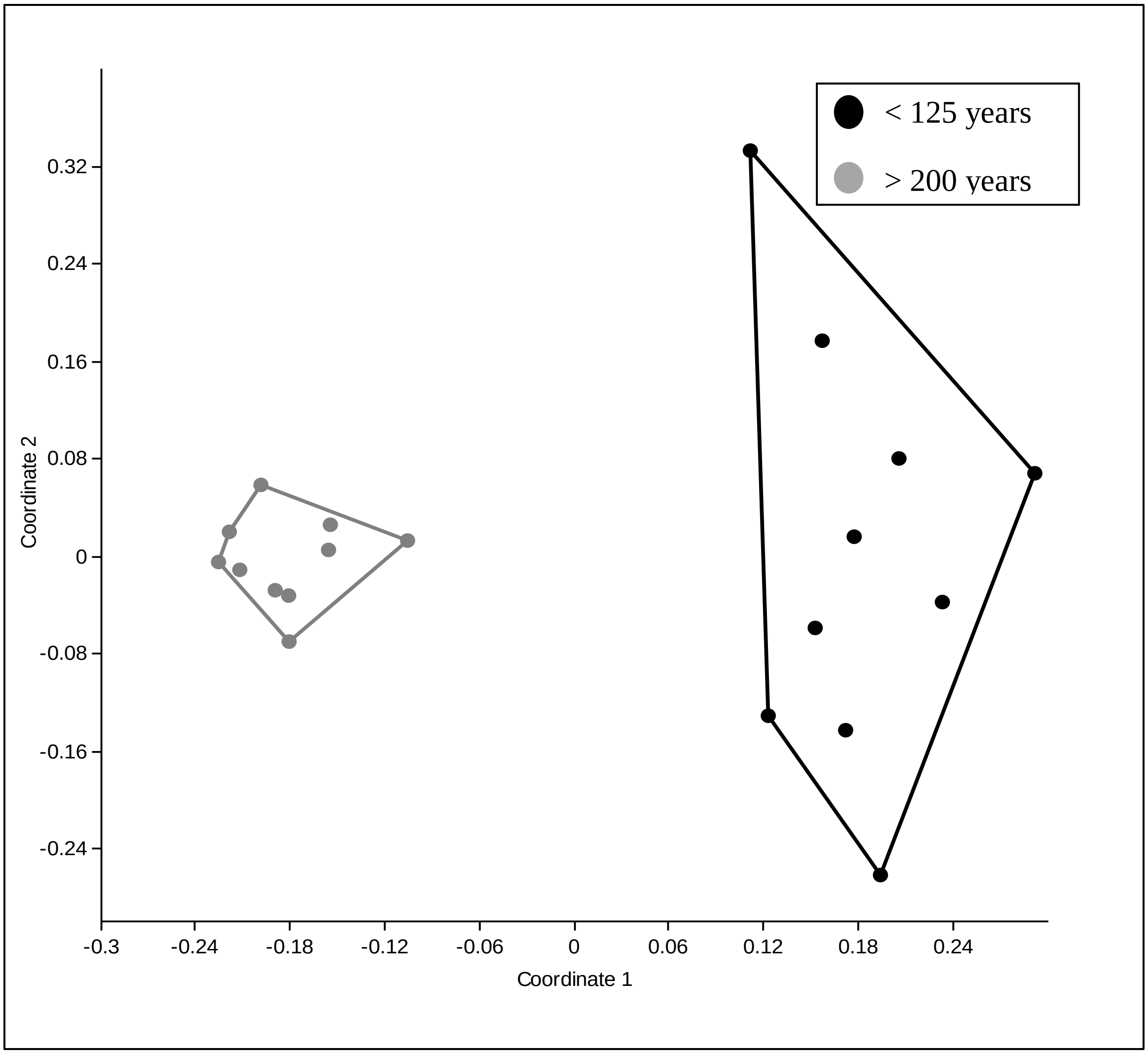

Figure I1. Land snail community structure in old-growth and second-growth forests based on Non-metric Multidimensional Scaling of the disturbance classes present in the Inner Bluegrass ecoregion (Stress = 17.71). Convex hulls are polygons enclosing all points within each group.

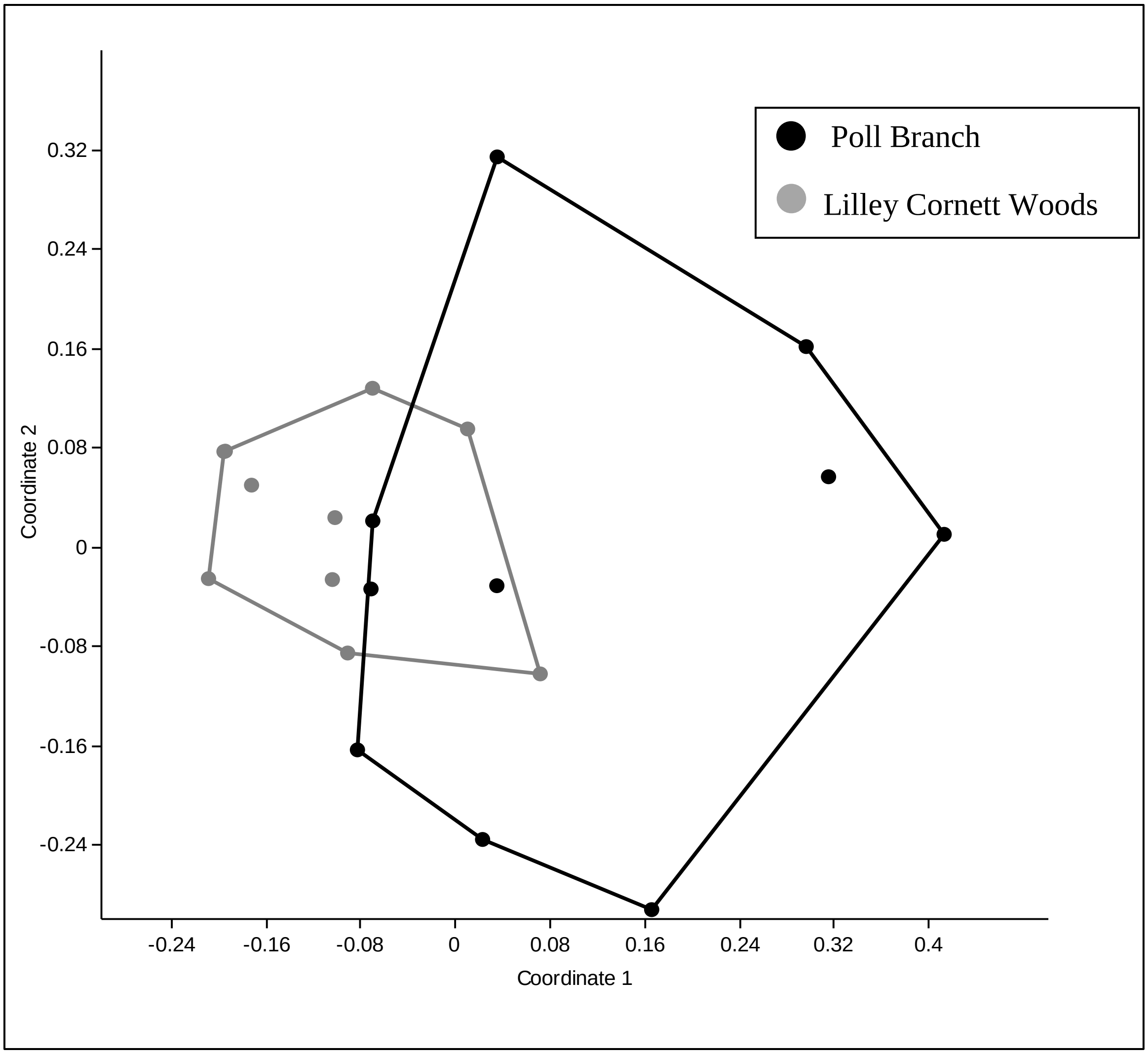

Figure I2. Land snail community structure in old-growth and second-growth forests based on Non-metric Multidimensional Scaling of the disturbance classes present at Lilley Cornett Woods and Poll Branch (Stress = 20.09). Convex hulls are polygons enclosing all points within each group.

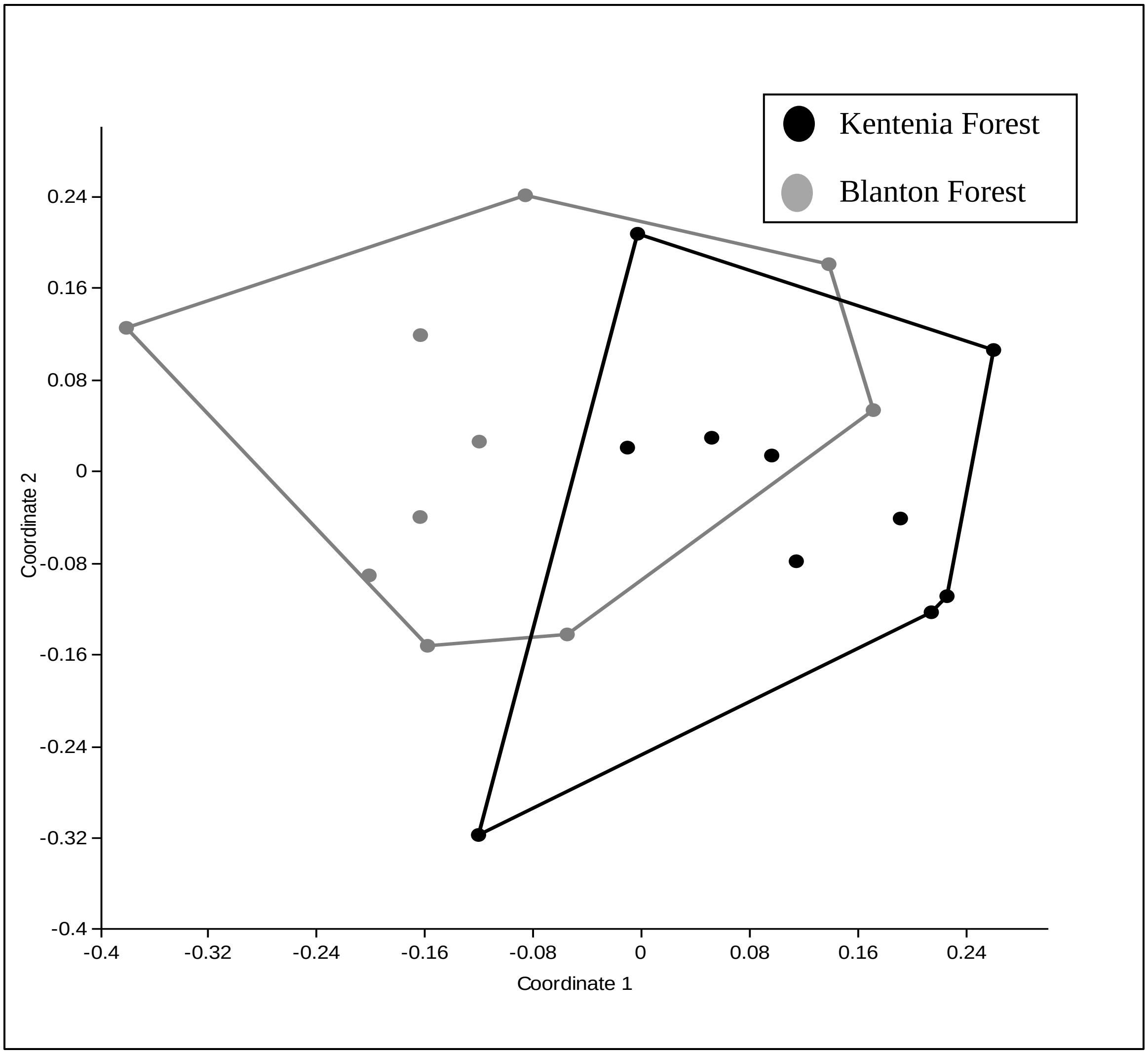

Figure I3. Land snail community structure in old-growth and second-growth forests based on Non-metric Multidimensional Scaling of the disturbance classes present at Blanton Forest State Nature Preserve and Kentenia State Forest (Stress = 26.38). Convex hulls are polygons enclosing all points within each group.