

Land snail diversity can reflect degrees of anthropogenic disturbance

DANIEL D. DOUGLAS,[†] DAVID R. BROWN, AND NEIL PEDERSON¹

Department of Biological Sciences, Eastern Kentucky University, Richmond, Kentucky 40475 USA

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Abstract. Faunal indicators of old-growth forests in heavily-disturbed regions are virtually non-existent. However, land snails, in particular micro-snails, could reflect the impact of land-use on ecosystem integrity. Because of their size, limited mobility, and propensity to spend their entire lives at one locality due to lack of migratory behavior, micro-snails are susceptible to changes in land-use within forested ecosystems. Therefore, we proposed the hypothesis that micro-snails would reflect land-use in forested ecosystems. We sampled snail communities in paired old-growth and second-growth forests in three distinct ecoregions. Species diversity, richness, and abundance were greater in two of the three old-growth sites compared to paired second-growth sites. Across all of the ecoregions, 21 out of 70 species had an affinity for old-growth. Eighteen of which were statistically significant. These results suggest that anthropogenic disturbance plays a key role in shaping species diversity and community structure of land snail fauna. However, site specific factors also appear to be important moderators of the response, and the mechanisms of the process remain to be studied. Snails appear to be a promising group of organisms to use as indicators of historic forest disturbance. In order to maintain ecological integrity, forest managers should consider management strategies that are low impact and protect existing patches of old-growth forests.

Key words: disturbance; ecosystem integrity; forested ecosystems; Kentucky; land snails; old-growth forests.

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¹ Present address: Tree Ring Laboratory of Lamont-Doherty Earth Observatory and Columbia University, Palisades, New York 10964 USA.

[†] **E-mail:** daniel.douglas@eku.edu

INTRODUCTION

Disturbance changes forest communities and alters ecosystem processes (Bormann and Likens 1979). Old-growth forests are among the best examples of ecosystems with little to no impact by humans and can be used as the best-available reference of historic conditions for managers and researchers. Though the definition of these forests is often debated (Leverett 1996), they are typically designated by characteristics of forest structure, landscape, and individual trees (Martin 1992, Pederson 2010). The most consistent

attributes of old-growth forests are large amounts of dead wood on the forest floor, little evidence of human logging or forest alteration, and presence of old and sometimes very large trees (Appendix B: Fig. B1). Typically, disturbance of old-growth forest alters structure by reducing the amount of dead wood, homogenizing the range of tree sizes, and reducing the presence of old trees (Oliver and Larson 1996). These alterations can impact ecosystem processes (Bormann and Likens 1979).

Many effects of anthropogenic disturbance are manifested on the forest floor. The herba-

ceous layer of forests takes centuries to recover to the diversity present in primary forests following disturbance (Wyatt and Silman 2010). Likewise, faunal communities of the forest floor do not return to previous abundances and assemblages because of changes in ecosystem structure (Petranka et al. 1993). These changes cause additional adverse effects including altering decomposition and nutrient cycling of organic material on the forest floor (Coleman et al. 2004).

Organisms with low dispersal capabilities, such as land snails, are susceptible to natural and anthropogenic disturbance (Strom et al. 2009). Micro-snails (<5 mm in diameter) appear to be particularly susceptible to disturbance due to their extremely limited dispersal capabilities (Baur and Baur 1988) and because they are dependent on microhabitats such as large accumulations of coarse woody debris (CWD) (Kappes et al. 2006). CWD is one of the most common and important characteristics of old-growth forests (Webster and Jenkins 2005). Old-growth also has high organic layer accumulations (Martin 1992), which provide moisture to micro-snails and prevent them from desiccating (Kappes et al. 2006). Because of the convergence between traits of micro-snails and old-growth forests, it would appear that micro-snails would have a preference for the more natural conditions of undisturbed ecosystems.

Here we investigate the effects of anthropogenic disturbances on land snail communities through the examination of mollusk diversity and community composition in mature second-growth and old-growth forests. We investigated environmental variables associated with disturbance that we suspected would influence land snail communities. Because of their perceived susceptibility to disturbance (i.e., lack of mobility, non-migratory behavior, habitat specialization), the null hypothesis is that there is no significant difference in diversity and composition between second-growth and old-growth forests. We also predicted that some micro-snail species would be indicators of old-growth forest conditions and reflect anthropogenic disturbance. Understanding the effects of anthropogenic activities on ecosystems will aid in developing management practices that will maintain ecological integrity.

METHODS

We conducted our study within three ecoregions of Kentucky, USA. Three paired old-growth and second-growth study sites within each ecoregion were selected to compare disturbance histories while controlling for variation in species distributions. We sampled at Floracliff State Nature Preserve (FSNP) within the Inner Bluegrass ecoregion. Much of the preserve was logged around the beginning of the 1990s and later used for agriculture. Despite these disturbances, sampling was conducted in an area containing numerous trees 200–400 years old and a second area with trees that are <125 years old (Pederson et al. 2012). Within the Appalachian Plateau ecoregion we sampled in Big Everidge Hollow, an old-growth forest that contains trees 300+ year old trees, at Lilley Cornett Woods Appalachian Ecological Research Station (LCW) and at Pole Branch, a second-growth forest paralleling Big Everidge Hollow that was clear-cut in 1945 and then contour-mined in 1970 (Muller 1982). On the Cumberland Mountain Thrust Block ecoregion we sampled at Blanton Forest State Nature Preserve (BFSNP), an old-growth forest containing three tree species 324–337 years old (Pederson et al. 2012), and at Kentenia State Forest (KSF), a second-growth forest that has experienced both fire and logging events. Detailed accounts of disturbance histories for KSF are not available.

We established 10 sampling plots of approximately one hectare within each study site. Plots were separated by at least 100 m and chosen based on walk-through surveys and knowledge of ecological requirements of land snails. Snails were sampled using leaf litter collections and visual searches. Leaf litter collections allowed quantification of micro-snails. We collected these samples in each plot by filling three one-liter cloth bags with leaf litter and detritus from throughout the plot. Litter was dried for one month and then sorted using #4, 10, 16, and 35 soil sieves. Macro-snails (>5 mm in diameter) were collected using visual searches of 20 person minutes per plot. Identification was based on morphology using taxonomic keys developed by Pilsbry (1940, 1946, 1948), Burch (1962), and Dourson (2010). Taxonomy was based on Turgeon and colleagues (1998).

Within each plot, we established a 20×20 m sub-plot to estimate percentages of canopy cover, bare ground, leaf litter, rock, CWD, soil pH, soil moisture, soil temperature, duff depth, aspect, and slope. A concave spherical densiometer was used to estimate curved linear canopy cover (Lemmons 1956). Duff depth was measured as the depth of the organic soil horizon (i.e., organic material accumulation from the bottom of the whole leaf layer to the bare mineral soil). Soil moisture and pH were measured using a Kelway soil tester at depth of approximately 5 cm. Soil temperature was measured with an Oakton Thermistor thermometer at approximately 5 cm deep, as well. We nested a 4×4 m plot within each 20×20 m plot to visually estimate percent density of shrubs at 0–1 m and 1–3 m height and percent cover of grasses and herbaceous plants.

We calculated Shannon-Weiner diversity (\log_e), Shannon-Weiner evenness, abundance, and community similarity between old-growth and second-growth using the Ecological Methodology software program (Krebs and Kenney 2009). We tested for differences in diversity, abundance, richness and evenness between old-growth and second-growth disturbance classes and among ecoregions using a random-effects factorial analysis of variance (ANOVA) in SPSS statistical software version 18. Error terms for all models were normal and homogeneous among groups. We used Tukey's post-hoc q statistic test to compare each ecoregion by disturbance regime. This approach has an inherent level of non-independence among sampling locations since our ecoregions are represented by just a single site; however, because old-growth sites are exceedingly rare and the sampling locations are geographically paired with nearby second growth sites, our results should be robust in terms of differences among disturbance classes.

We analyzed species composition using non-metric multidimensional scaling (NMS) with PC-ORD 6 (McCune and Mefford 2011). NMS is an unconstrained ordination and was used in this study to reveal variance structure among snail species, irrespective of any environmental gradients. This graphically depicts the degree of overlap or separation of ecoregions and disturbance classes based on species data alone, and thus we conducted this analysis on all ecoregions combined. NMS is appropriate for sparse species matrices because it

uses rank-distances to avoid assumptions of linearity (McCune and Grace 2002). We used Bray-Curtis dissimilarity to construct the distance matrix with 250 iterations (repetitions) to approximate the results more closely. The number of axes was selected based on permutation analysis that compared stress values of runs of data with runs of randomized data.

We conducted a Multiple Response Permutation Procedure (MRPP) with PC-ORD 6 to test for differences in species composition between second-growth and old-growth forest. A Bray-Curtis dissimilarity measure was performed on each ecoregion.

We conducted Indicator Species Analysis within ecoregions separately for each disturbance class using PC-ORD 6. This analysis combines relative abundances and frequencies to estimate concentrations of species abundances and the reliability of occurrence of species to defined classes. Indicator values (IV) range from 0–100. A value of 100 occurs when a species is exclusively found in one disturbance class. We used a Monte Carlo test with 4999 randomizations, to test for statistical significance of each species as an indicator.

We conducted Canonical Correspondence Analysis (CCA) on each ecoregion to assess habitat associations of land snails using Program R 2.15.0, Package Vegan (R Development Core Team 2012). CCA defines the variation in snail communities based on environmental variables and provides a test of the relationship between environmental variables and snail communities. Thus, it differs from NMS which is an unconstrained analysis of the ordered relationships among species that does not incorporate relationships with explanatory environmental variables. We used a stepwise procedure to remove inter-correlated environmental variables while keeping variables that had high correlations with snail community data. A Monte Carlo permutations test with 1000 iterations was used to test the null hypothesis that there was no relationship between the species community matrix and environmental variable matrix.

RESULTS

Snail sampling yielded 3265 individual snails, representing 15 families, 35 genera, and 70

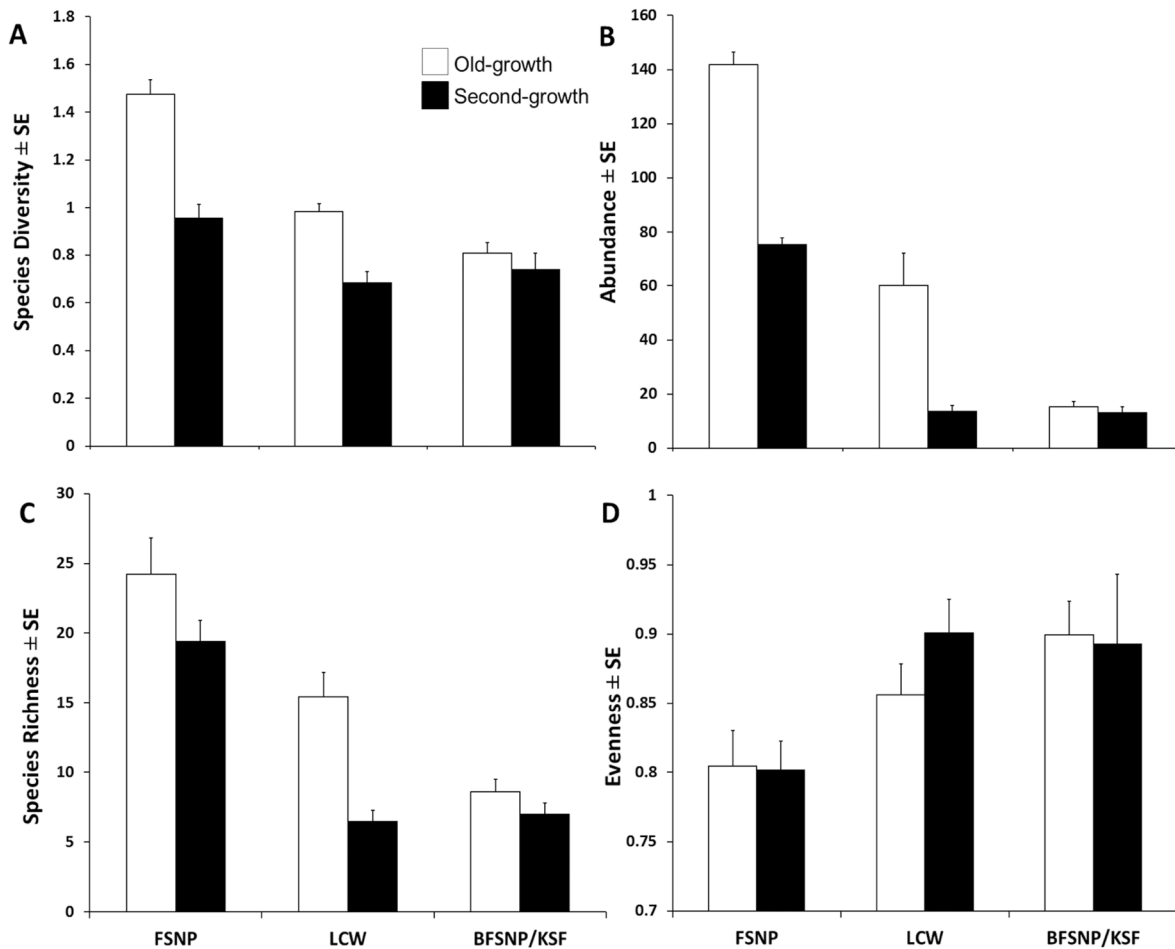


Fig. 1. Species diversity (A), abundance (B), richness (C), and evenness (D) for each set of paired study sites. FSNP = Floracliff State Nature Preserve, LCW = Lilley Cornett Woods Appalachian Ecological Research Station, and BFSNP/KSF = Blanton Forest State Nature Preserve/Kentonia State Forest.

species (Appendix A: Table A1), none of which were exotic species. Shannon-Weiner diversity was higher in the FSNP and LCW old-growth forests compared to paired second-growth sites (Fig. 1) (ANOVA disturbance \times ecoregion: $F_{2,54} = 9.29$, $p < 0.001$; FSNP: $q_{54} = 4.70$, $p < 0.001$; LCW: $q_{54} = 6.96$, $p < 0.001$). Diversity of BFSNP old-growth forest did not differ compared to its paired second-growth site ($q_{54} = 0.93$, $p = 0.939$). Species richness was higher in the FSNP and LCW old-growth forests compared to paired sites (Fig. 1) (ANOVA disturbance \times ecoregion: $F_{2,54} = 6.56$, $p = 0.003$; FSNP: $q_{54} = 5.73$, $p < 0.001$; LCW: $q_{54} = 2.23$, $p < 0.02$). The BFSNP old-growth forest did not differ in richness compared to the paired KSF second-growth ($q_{54} = 0.74$, $p = 0.97$).

Abundance was higher in FSNP and LCW old-growth forests compared to their paired second-growth site (Fig. 1) (ANOVA disturbance \times ecoregion: $F_{2,54} = 9.50$, $p < 0.001$; FSNP: $q_{54} = 5.49$, $p < 0.001$; LCW: $q_{54} = 5.67$, $p < 0.001$). The BFSNP old-growth forest did not differ in abundance compared to the paired KSF second-growth site ($q_{54} = 0.24$, $p = 1.00$). Shannon evenness values were similar between all paired old-growth and second-growth forests (Fig. 1) (ANOVA: disturbance \times region $F_{2,54} = 0.674$, $p = 0.51$; FSNP: $q_{54} = 1.30$, $p = 0.78$; LCW: $q_{54} = 0.07$, $p = 1.00$; BFSNP/KSF: $q_{54} = 2.18$, $p = 1.00$), indicating that species collected were evenly distributed throughout both disturbance classes within each study site and that differences in

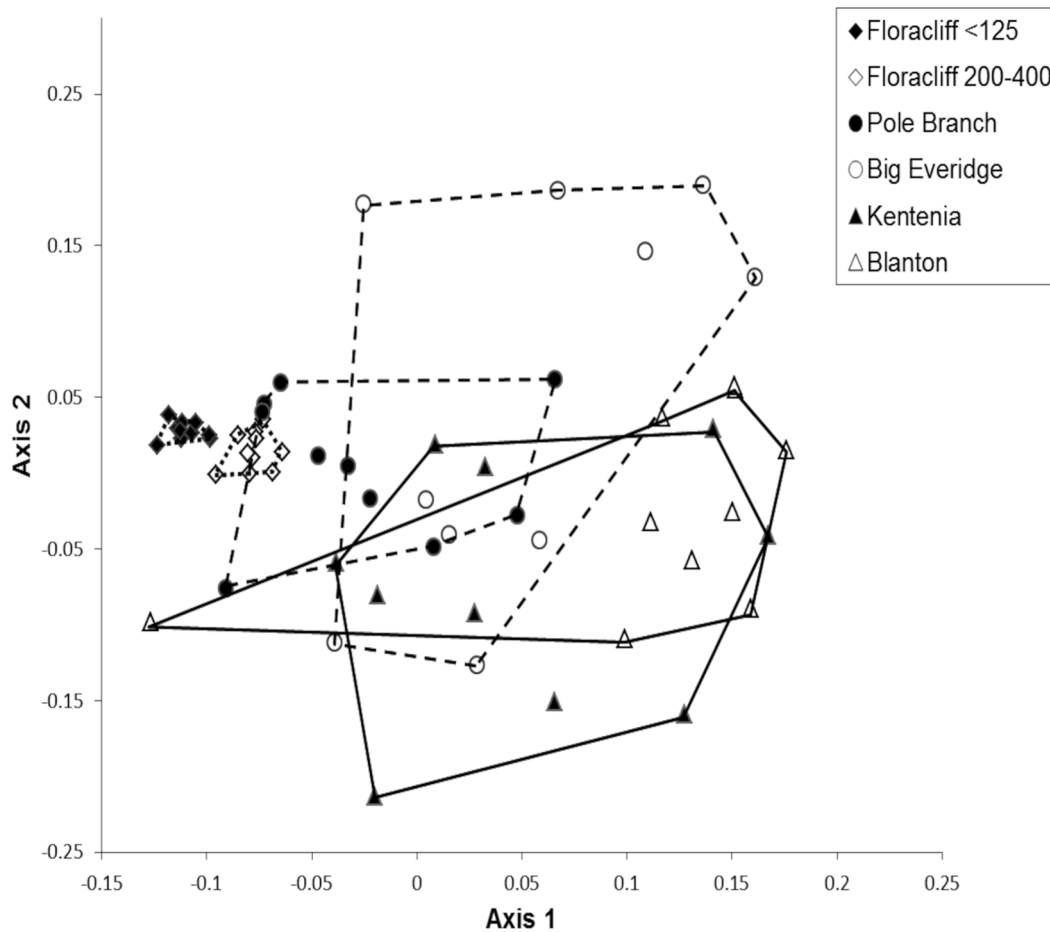


Fig. 2. Non-metric multidimensional scaling ordination of land snail community structure in old-growth and second-growth forests in central and eastern Kentucky, USA. Open symbols represent old-growth forest sites while filled symbols represent second-growth forest sites.

diversity between disturbance regimes were driven primarily by species richness.

Strong differences in species composition among the three ecoregions across all 60 sites were indicated by NMS ordination (Fig. 2) (final stress = 0.21). The degree of separation of communities between disturbance regimes varied among ecoregions. Clear separation was observed between FSNP old-growth and second-growth forest while there was some overlap between the forest types at LCW and BSNP/KSF. Nonetheless, separation is apparent between old-growth and second-growth forest at LCW and BSNP/KSF.

MRPP analysis revealed significant differences in species composition concentrations between

second-growth and old-growth forest with all ecoregions combined ($p < 0.004$, chance-corrected within-group agreement $A = 0.02$). When ecoregions were examined separately, all sites showed significant differences in the concentrations between disturbance classes (FSNP: $A = 0.17$, $p < 0.001$; LCW: $A = 0.06$, $p < 0.0001$; BSNP/KSF: $A < 0.001$, $p < 0.001$).

When ecoregions were examined separately, indicator species analysis showed 18 species had statistically significant affinity for old-growth (Table 1). Fourteen of these species were microsnails with *Carychium exile* I. Lea, 1842 being the strongest indicator of old-growth forests (indicator status = 0.65, $p < 0.01$). Conversely, *Triodopsis tridentata* (Say, 1816) was the strongest indicator

Table 1. Indicator species for old-growth/less disturbed conditions for three ecoregions of eastern and central Kentucky. Indicator values are presented \pm SD for each ecoregion. The p-values are from analyses conducted across all ecoregions studied. FSNP = Floracliff State Nature Preserve, LCW = Lilley Cornett Woods Appalachian Ecological Research Station, and BFSNP/KSF = Blanton Forest State Nature Preserve/Kentonia State Forest

Species	FSNP	LCW	BFSNP/KSF	p
<i>Carychium clappi</i>	60 \pm 2.47	65 \pm 9.64		0.04
<i>Carychium exile</i>	61 \pm 2.66	90 \pm 10.08	70 \pm 10.00	<0.001
<i>Carychium nannodes</i>	60 \pm 2.27	75 \pm 11.57		0.01
<i>Cochilocopa moreseana</i>	70 \pm 6.61	56 \pm 9.20		0.001
<i>Collumella simplex</i>	86 \pm 7.61			<0.001
<i>Gastrocopta armifera</i>	85 \pm 7.47			0.03
<i>Gastrocopta contracta</i>	87 \pm 8.25			0.01
<i>Gastrocopta pentodon</i>	68 \pm 8.59			0.03
<i>Gastrocopta procera</i>	100 \pm 9.18			0.001
<i>Gastrodonta interna</i>	88 \pm 7.88			0.01
<i>Glyphyalinia indentata</i>	64 \pm 7.18	56 \pm 9.02		0.01
<i>Glyphyalinia wheatleyi</i>	72 \pm 8.24			0.28
<i>Guppya sterkii</i>	69 \pm 7.89			0.03
<i>Haplotrema concavum</i>	73 \pm 8.15			<0.01
<i>Hawaii miniscula</i>	65 \pm 7.18	56 \pm 9.11		0.04
<i>Mesomphix cupreus</i>	70 \pm 8.99			0.04
<i>Patera appressa</i>		50 \pm 8.82	50 \pm 8.58	<0.01
<i>Punctum minutissimum</i>		69 \pm 9.54		0.46
<i>Striatura ferrea</i>				<0.01
<i>Vallonia exentrica</i>	70 \pm 8.71			0.01
<i>Vertigo parvula</i>		60 \pm 8.99		0.24

of second-growth forests, but its indicator status was not statistically significant (indicator status = 0.31, $p = 0.17$).

The final CCA models each included two significant axes and three environmental variables that were correlated with snail communities. Stepwise modeling indicated that bare ground was important at LCW and BFSNP/KSF. However, we removed it from the analysis; after inspection of the data revealed that the percent bare ground was extremely low at both areas and within both disturbance classes (mean \pm SE = 1.32 \pm 0.56) such that sampling error may have led to spurious, biologically irrelevant results for that variable. CCA models showed that environmental variables explained 20.3% of the total variation in snail communities at FSNP, 21.8% at LCW, and 21.8% at BFSNP/KSF (Fig. 3). Depth of the duff layer was correlated with snail community structure in all three ecoregions, and elevation was correlated at FSNP and BFSNP/KSF. Although these vectors in particular paralleled differences among disturbance classes, the direction of the relationships differed among ecoregions. Other important environmental variables included pH, slope, rock cover, and coarse woody debris.

DISCUSSION

Our results show that land snails, especially micro-snails, are sensitive to changes associated with human disturbance. We found strong differences between second-growth and old-growth forest in species diversity and community structure of land snails. Although the exact mechanisms are as yet unclear, it is extremely likely that past anthropogenic disturbance played a key role. Eighteen species, including 14 micro-snails, were significant indicators of forest with little or no anthropogenic disturbance histories. These results highlight the need for understanding the long-term impacts of disturbance and recovery in forested ecosystems at all trophic levels, not simply the more charismatic groups. Our results suggest that forest disturbance, particularly from human land-use, can alter land snail communities and diversity for decades. Because of the foundational ecosystem role of snails, these changes could ultimately compromise ecosystem integrity. These results strongly suggest that micro-snails could be important and consistent indicators of old-growth forests.

Due to the fact that land snails are important

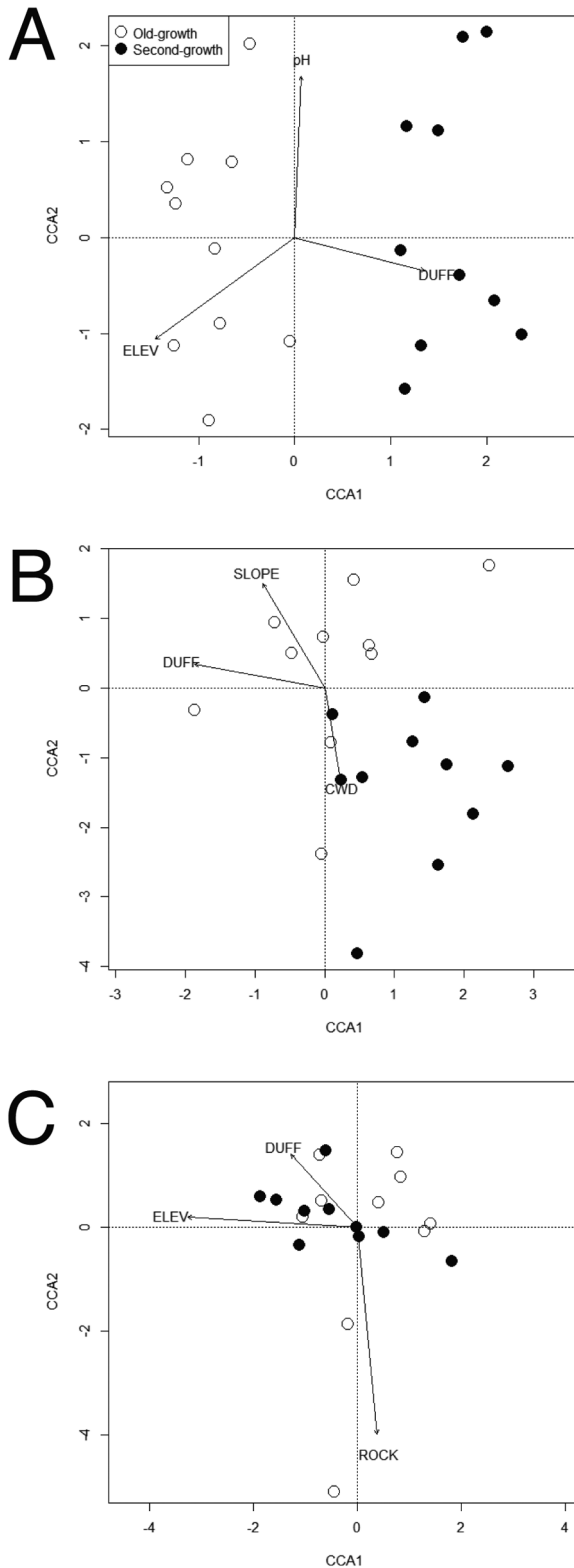


Fig. 3. Canonical Correspondence analysis (CCA) output for Floracliff State Nature Preserve (A), Lilley

organisms involved in regulating decomposition through the movement of fungi (Caldwell 1993) and nutrient cycling (Pearce 2008), they can be considered among the most important organisms for carrying out essential ecosystem processes. Thus, it is crucial to know the effects of disturbance to understand which species will survive given the expected continuation of ecosystem alteration. If particular species or species assemblages are responsible for carrying out biological processes, then it is important that these interactions are understood. Due to the lack of study and uncertainty pertaining to how climate change will affect these organisms, it is important to know what role habitat degradation will play in species assemblages in forests of the eastern US as well as how the loss of these organisms will affect ecosystems.

Fourteen of the 18 indicator species were micro-snails. This leaves four macro-snail species with positive indicator status for old-growth forests. Because of their ability to disperse more readily than micro-snails, it is more difficult to explain the indicator status of the four remaining macro-snail species. Because of their larger size, these species should be good dispersers, in relation to micro-snails, and poor indicators of forest disturbance. It is possible that these species have different life history traits from other macro-snails that would limit colonization, but a lack of basic research on snail populations limits such speculation.

Dispersal from refugia following a disturbance is likely to be an important process affecting land snail community composition. In areas with severe and repeated disturbances, refugia are likely limited. The rate of re-colonization of disturbed areas from refugia is poorly understood, but the frequency and severity of disturbance, as well as depth of refugia, are likely important to the long-term persistence of populations (Kiss et al. 2004). Repeated disturbances

Cornett Woods (B), and Blanton and Kentenia Forests (C) plotted in ordination space and based on habitat parameters. Habitat parameters that explain the most variation in the data are represented by a joint plot with labeled vectors. CWD = % coarse woody debris, DUFF = depth of duff accumulation, ELEV = elevation, ROCK = % rock, and SLOPE = % slope.

may create small, isolated populations with limited gene flow, and poor quality habitat that, when coupled with stochastic events, could lead to an increased probability of localized extinctions (Hylander et al. 2005). Community composition and structure will depend on recolonization from surrounding undisturbed forests, which will be influenced by dispersal abilities, vegetation characteristics, and environmental conditions in the landscape.

The differences we find between disturbance histories are likely moderated by ecoregion, degree of disturbance, and site-specific variation including different succession trajectories (Raheem et al. 2009). Old-growth and second-growth sites at FSNP were clearly separated by the NMS, which may be attributable to the higher degree of historic disturbance at that site. One interesting result here is that some environmental variables that are known to be important for land snails, and differ between old-growth and second-growth forests, such as the density of coarse woody debris, are not the strongest and most consistently correlated variables with snail communities in this study. It is possible that some variables not quantified here, such as microclimate or nutrient availability, influenced post-disturbance communities and that these differences could be found to be greater in more intensive studies where elevation, aspect, and slope are better controlled. Another surprising and somewhat confusing result was that duff depth tended to be higher in second-growth sites at FSNP and related to snail communities there. The second-growth sites at FSNP tended to have lower slope and more understory shrubs, which could lead to higher litter accumulation (Douglas, Brown, Pederson, *personal observations*). At LCW, duff was related to snail communities, however, it was found to be deeper in the old-growth forest, a pattern described by other researchers (Martin 1992). We also found that elevation was related to snail communities, but in opposite directions relative to disturbance classes. We attribute this to site specific characteristics; specifically, at FSNP all of the second-growth sites were higher in elevation than old-growth sites (average difference = 14 m, range = 55 m), whereas the second-growth sites at BFSNP/KSF were almost all lower elevation than the old growth sites. These results suggest that forest

disturbance causes complex responses to environmental characteristics, which, in turn, likely lead to complex snail community responses. Regardless, across three ecoregions we consistently found that disturbance of old-growth forest leaves a legacy of different snail communities.

Although we have limited site-level replication within each ecoregion, our results suggest interesting and predictable patterns among ecoregions. It is also possible that differences in community composition between disturbance regimes and ecoregions are related to the substrate and forest composition. FSNP is underlain by limestone, whereas the other two study sites are composed primarily of sandstone. Because land snails require calcium sources for basic physiological and biological processes (Fournié and Chétail 1984), and calcium availability affects the presence of land snails (Hotopp 2002, Skeldon et al. 2007), limestone areas typically have relatively high abundances of snails (Schilthuizen et al. 2003, Jurickova et al. 2008). While this may explain the high abundance and species richness of snails at FSNP, a site does not require limestone for high species richness. For example, LCW, with sandstone geology, had more total species across all sample plots ($N = 53$) than FSNP ($N = 50$) (Appendix A). The high diversity at this site may be driven by favorable biotic factors and heterogeneous microclimatic conditions, which might also explain why the average species richness among sample plots was lower at LCW than at FSNP, in contrast to the cumulative site-wide species richness.

Most of the sampling points at LCW were located in a mesic hardwood forest that has some tree species, like flowering dogwood (*Cornus florida* L.), that act as sources of calcium by extracting it from the soil, directing it to leaves and distributing it to the forest floor through leaf abscission (Nation 2007). Due to the fact that some forest management practices, such as clear-cutting, will affect calcium levels (McLaughlin and Wimmer 1999), landscapes with high calcium sources may be more sensitive to anthropogenic disturbance.

Human disturbances, including forestry, can increase the probability of invasion by exotic earthworms (Hendrix and Bohlen 2002). Invasive earthworms influence the composition of organic

material and nutrient content available on the forest floor (Greiner et al. 2012), and will likely impact habitat for litter-dwelling organisms like land snails. During this study, earthworms were only observed at FSNP and at LCW. However, earthworms were only recently observed in a part of the old-growth forest at LCW (Douglas, *personal observation*) and they were not observed at BFSNP/KSF. It might be that earthworms are present at BFSNP/KSF, but an earlier study indicated only indigenous oligochaetes existing at these sites (Kalisz and Powell 2000). We do not know if the earthworms present at these sites are invasive, but it would not be a surprising discovery since invasive species (e.g., non-native plants and hemlock woolly adelgid) have recently begun to appear in this region (Spaulding and Rieske 2010, Chapman and McEwan 2012, Chapman et al. 2012).

The eastern hemlock (*Tsuga canadensis* L.) dominated sampling sites at BFSNP/KSF might be an important factor for their relatively low snail diversity. Sampling in BFSNP/KSF sites was mostly focused in hemlock forests, unlike FSNP and LCW, which could have played a role in the lack of difference between disturbance histories. Hemlock-dominated communities have low calcium availability and low pH, which could limit snail diversity and abundance. Snail species inhabiting acidic communities may be more tolerant of adverse conditions than species in hardwood-dominated forests (Archer 1942). Because of this, hemlock-associated snail species may be better adapted to disturbance, enabling more rapid re-colonization and recovery compared to species that inhabit hardwood forests.

Other environmental factors including vegetation, micro-environmental conditions, canopy cover, and ground cover might affect re-colonization of terrestrial snails following disturbance and should be studied within the context of disturbance. The density of the vegetation can affect micro-habitat conditions (Geiger et al. 2009), which influence dispersal (Boag 1985). Adverse climatic conditions (e.g., drought) following disturbance adversely affect micro-habitat and cause local extinctions (Chang and Emlen 1993). Disturbance can have strong and lasting effects on leaf litter parameters, herbaceous layer recovery, and CWD (Webster and Jenkins 2005). These habitat parameters will influence plant

species composition, desiccation rates of organic material, and potential for land snails to re-colonize an area (Martin and Sommer 2004).

Using our findings, forest managers should consider techniques that include green tree retention and leaving CWD intact to maintain the integrity of land snail communities. A mixed strategy that considers stand rotation lengths as well as disturbance severity and spatial scale will likely be required to maintain biodiversity and prevent species extirpations. This concept is demonstrated at FSNP where the older forest had significantly greater land snail biodiversity. Both FSNP study forests were likely selectively logged at the beginning of the 1900s. However, age structure of the younger forest (Pederson et al. 2012) and current physical structure indicates that it experienced great disturbance severity. Of the five trees cored in the younger forest, the average age was 146.8 years, while the average age in the older section among the 15 cored trees was 295.0 years (Pederson et al. 2012). Our findings suggest that land snails may be extirpated from forests that are managed through intensive forestry (i.e., clear-cutting) at large scales. These losses could cascade through trophic levels with a local loss or reduction of narrowly distributed habitat specialists.

We find that older and less disturbed forests contain greater land snail diversity than younger forest and that species diversity and community structure is strongly influenced through anthropogenic disturbance. Thus, older and less disturbed forests are likely important for preserving biological diversity. This conclusion strengthens arguments regarding the high value of old-growth for scientific research and historical significance. Faunal indicators of old-growth have been explored for many decades, with minimal success. Here, we present significant evidence that micro-snails are useful indicators of old-growth forests. These results are not only applicable to the forests of the eastern United States, but likely also apply in temperate forests worldwide.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Species of land snails collected with abundances per site during this study. FSNP = Floracliff State Nature Preserve, LCW = Lilley Cornett Woods Appalachian Ecological Research Station, and BSNP/KSF = Blanton Forest State Nature Preserve/Kentonia State Forest.

Species	Study sites		
	FSNP	LCW	BSNP/KSF
Carychiidae			
<i>Carychium clappi</i> Hubricht, 1959	238	79	51
<i>Carychium exile</i> I. Lea, 1842	240	140	13
<i>Carychium nanmodes</i> G.H. Clapp, 1905	226	87	12
Cochilicopidae			
<i>Cochilicopa moreseana</i> (Doherty, 1878)	51	20	7
Discidae			
<i>Anguispira alternata</i> (Say, 1816)	34		
<i>Anguispira kochi</i> (Pfeiffer, 1821)	54		
<i>Anguispira mordax</i> (Shuttleworth, 1852)		4	3
<i>Discus patulus</i> (Deshayes, 1830)	32	43	6
Haplotrematidae			
<i>Haplotrema concavum</i> (Say, 1821)	43	20	4
Helicarnidae			
<i>Euconulus fulvus</i> (Muller, 1774)	20	2	
<i>Guppya sterkii</i> (Dall, 1888)	34	21	
Helicodiscidae			
<i>Helicodiscus notius</i> Hubricht, 1962	22	1	
Philomycidae			
<i>Palifera dorsalis</i> (A. Binney, 1885)			1
<i>Philomycus carolinensis</i> (Bosc, 1802)		1	1
Polygyridae			
<i>Appalachina sayana</i> (Pilsbry, 1906)	51	5	5
<i>Euchemotrema fraternum</i> (Say, 1824)	42	6	4
<i>Inflectarius inflectus</i> (Say, 1821)	22	4	
<i>Inflectarius rugeli</i> (Shuttleworth, 1852)	17	6	6
<i>Mesodon elevatus</i> (Say, 1821)	26		
<i>Mesodon normalis</i> (Pilsbry, 1900)		8	10
<i>Mesodon thyroidus</i> (Say, 1816)	20		
<i>Mesodon zaleatus</i> (A. Binney, 1837)	20	1	
<i>Neohelix albolabris</i> (Say, 1816)	19	4	
<i>Patera appressa</i> (Say, 1821)	28	8	9
<i>Stenotrema angellum</i> Hubricht, 1958	16		
<i>Stenotrema barbatum</i> (G.H. Clapp, 1904)	14		
<i>Stenotrema stenotrema</i> (Pfeiffer, 1842)	12	13	4
<i>Triodopsis tridentata</i> (Say, 1816)	16	43	6
<i>Xolotrema denotatum</i> (Ferussac, 1821)	20	2	2
Pomatiopsidae			
<i>Pomatiopsis lipadaria</i> (Say, 1817)	15	3	1
Punctidae			
<i>Punctum minutissimum</i> (I. Lea, 1841)	22	15	7
Pupillidae			
<i>Columella simplex</i> (Gould, 1841)	70	4	
<i>Gastrocopta armifera</i> (Say, 1821)	78	2	
<i>Gastrocopta contracta</i> (Say, 1822)	79	17	1
<i>Gastrocopta contricaria</i> (Say, 1816)		1	
<i>Gastrocopta pentodon</i> (Say, 1821)	45		
<i>Gastrocopta procera</i> (Gould, 1840)	71		
<i>Pupoides albilabris</i> (C.B. Adams, 1841)	13	1	
<i>Vertigo bollesiana</i> (E.S. Morse, 1875)		8	9
<i>Vetigo gouldii</i> (A. Binney, 1843)		2	
<i>Vertigo parvula</i> Sterki, 1890		7	
<i>Vertigo tridentata</i> Wolf, 1870	32		
Strobilsopsidae			
<i>Stobilops aenea</i> Pilsbry, 1926	19	1	
<i>Strobilops labyrinthica</i> (Say, 1817)	15		

Table A1. Continued.

Species	Study sites		
	FSNP	LCW	BSNP/KSF
Succineidae			
<i>Catinella oklahomarum</i> (Webb, 1953)	226		
Valloniadae			
<i>Vallonia excentrica</i> Sterki, 1893	12		
Zonitidae			
<i>Gastrodonta interna</i> (Say, 1822)	78	10	2
<i>Glyphyalinia cryptomphala</i> (G.H. Clapp, 1915)		4	
<i>Glyphyalinia indentata</i> (Say, 1823)	38	17	11
<i>Glyphyalinia wheatleyi</i> (Bland, 1883)	41	30	17
<i>Hawaii miniscula</i> (A. Binney, 1840)	51	15	2
<i>Mesomphix cupreus</i> (Rafinesaue, 1831)	16		2
<i>Mesomphix inornatus</i> (Say, 1821)	23	39	11
<i>Mesomphix perlaevis</i> (Pilsbry, 1900)	31	2	
<i>Paravitrea capsella</i> (Gould, 1851)	18	15	4
<i>Paravitrea multidentata</i> (A. Binney, 1840)		8	
<i>Paravitrea placentula</i> (Shuttleworth, 1852)		3	
<i>Striatura meridionalis</i> (Pilsbry and Ferriss, 1906)	30	4	
<i>Striatura ferrea</i> E.S. Morse, 1864		14	
<i>Ventridens demissus</i> (A. Binney, 1843)		7	19
<i>Ventridens gularis</i> (Say, 1822)		34	36
<i>Ventridens intertextus</i> (A. Binney, 1841)	15	4	14
<i>Ventridens lasmodon</i> (Phillips, 1841)		1	
<i>Ventridens lawae</i> (W.G. Binney, 1892)		2	2
<i>Ventridens ligera</i> (Say, 1821)	21	2	
<i>Ventridens theloides</i> (Walker and Pilsbry, 1902)		2	
<i>Zonitoides arboreus</i> (Say, 1816)	19	1	2
<i>Zonitoides elliotti</i> (Redfield, 1856)		2	
Abundance	2188	793	284
Species Richness	50	53	33

APPENDIX B



Fig. B1. Images from old-growth forests used in this study. Image (A) is a stand at Floracliff State Nature Preserve containing trees 320–370 years old (Photo: N. Pederson). Image (B) is a stand in Big Everidge Hollow at Lilley Cornett Woods which contains trees that are 300+ years old (Photo: D. Douglas). Image (C) is a stand at Blanton Forest State Nature Preserve that contains 324–337 year old trees (Photo: N. Pederson). All images show uneven diameter trees (suggesting uneven age classes), standing snags, coarse woody debris present on the forest floor, sinuous trees, and topography consistent with the defining characteristics of old-growth forests. These structural attributes are in strong contrast to the second-growth forests used in this study.