SOIL SEED BANKS IN MIXED OAK FORESTS OF SOUTHEASTERN OHIO

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Effects of Forest Management Regime on Soil Seed Bank Composition in Mixed Oak Forest of Southeastern Ohio (67 pp.)

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The effects of common forest management practices (burning and thinning) on the seed bank are assessed. Species composition of the soil seed bank is examined under three treatments: thin, burn, thin followed by burning, and an untreated control. Thinning was conducted in Fall 2000 and burns were conducted in Spring 2001. Soil samples were collected in March 2004, 3 years following treatment. Species composition is assessed by seedling emergence. Seventy total species are found in the seed bank. Ruderal species such as *Erechtites hieraciifolia* (L.) Raf., *Carex* spp., and *Rubus* spp. are the most commonly occurring species across all treatments. No significant difference in species composition or proportion of functional groups is found between any of the treatment groups. Species composition of the seed bank and above-ground vegetation are significantly different in all treatments. Species composition and canopy cover are each significantly spatially autocorrelated in the thinned and burned treatment.

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Introduction

Vegetation dynamics in forested ecosystems are dependent upon the availability of propagules of individual species. Plants can propagate themselves by vegetative or sexual reproduction, with many species using a combination of these strategies (Bierzychudek 1982). The soil seed bank serves as a propagule storage system. Buried propagules (comprising both perennial roots and rhizomes, and the soil seed bank) are very important to species establishment (Marks and Mohler 1985).

The soil seed bank consists of viable, ungerminated seeds that are stored in the soil (Bigwood and Inouye 1988). These seeds enter the soil seed bank as they are produced by local plants and fall to the ground, or disperse into an area (Harper 1977). Thompson and Grime (1979) divided the soil seed bank into two types – transient and persistent. Transient seed banks are those in which the seeds do not remain viable for more than one year, while persistent seed banks consist of seeds that persist and remain viable in the soil longer than one year. Thompson (1993) further divided the persistent seed bank into short-term (lasting 1-5 years in the soil) and long-term (remaining viable in the soil for more than 5 years). A recent comparison of conceptual models of the soil seed bank re-affirmed the usefulness of Thompson and Grime's (1979) system and Thompson's (1993) system (Csontos and Tamás 2003).

Each plant species has a particular seed banking strategy, ranging from no seed storage in the soil to seeds that persist in the soil for many years (Nakagoshi 1985). Thus, the "soil seed bank" of an area or community is composed of the overlapping seed banks of all species present in that area. Once they have entered the soil seed bank, seeds can leave it by germinating or dying. Seed death can occur in several ways, including: predation, being attacked by a fungus or other pathogen, mortality due to fire or flooding, or natural senescence with old age (Baskin and Baskin 1998).

Properties of forest soil seed banks

The species composition of the soil seed bank depends on the current above-ground species composition and historical land-use of an area. Soil seed banks of old-growth forests tend to contain primarily forest species, with spring ephemerals notably absent, and tree species rarely included (Leckie *et al*. 2000). The seed banks of second-growth forests growing on formerly cultivated land tend to have soil seed banks more closely resembling those of old fields, though these old-field species may or may not be present in the current above-ground vegetation (Pickett and McDonnell 1989, Hyatt and Casper 2000). In contrast to post-agricultural forests, second growth forests regenerating after non-agricultural disturbance (logging, fire, etc.) tend to lack old-field species, trees, and shrubs, but be dominated by forest herbs, graminoids, and ruderals (Scheiner 1988, Schiffman and Johnson 1992).

The life form types that are present in the community also influence the composition of the soil seed bank. Woody species tend to have transient seed banks, particularly in temperate climates (Thompson 1992). However, those that do have persistent seed banks are generally early successional, short-lived species such as *Rubus* spp. (Thompson 1992). These species tend to germinate in canopy gaps, where light availability is enhanced. Shade-tolerant forb species also do not commonly maintain a soil seed bank (Brown and Oosterhuis 1981, Roberts 1981, Thompson 1992, Bossuyt *et al*. 2002). Forest seed banks are often dominated by ruderal species, which are disturbance-adapted and respond well to high-light environments (Bossuyt *et al*. 2002).

The composition of the soil seed bank is influenced by the existing above-ground vegetation. The understory layer in eastern deciduous forests is quite diverse, and is composed of forb species, woody species including shrubs and seedlings of canopy species, and graminoids (Sutherland *et al*. 2003). The herbaceous species composition undergoes shifts through the course of the year, with spring ephemerals dominant early on, and graminoids and composites dominant later in the season (Small and McCarthy 2002*a*).

Clear differences between the species composition of the above-ground vegetation and the soil seed bank have been found in a number of systems, including disturbed and undisturbed pine and hardwood second-growth forests, and marshes (Olmsted and Curtis 1947, Harper 1977, Scheiner 1988, Morgan and Neuenschwander 1988, Wilson *et al.* 1993, Carter and Ungar 2002). Differences result both from the presence of species above-ground that do not maintain a soil seed bank and from the presence of species in the seed bank (usually ruderal or old-field species) that are not present above-ground (Oosting and Humphreys 1940, Thompson 1992). When the seed bank is divergent from the above-ground vegetation, disturbances that trigger a release of germination from the seed bank may result in a change in the above-ground species composition (Wilson *et al*. 1993).

Ecological function of soil seed banks

The soil seed bank is an important component of the forest, which may impact several aspects of ecological functioning, including genetic, population, and community-level dynamics (Hyatt and Casper 2000). The soil seed bank can influence the genetic variation of a plant population by acting as a buffer to changes in a population's genetic composition that might arise from major fluctuations in population size. Even in years with few individuals surviving to reproductive age, the reproductive efforts of other (genetically different) individuals are present via germination from the stored seed bank – potentially making the genetic pool larger than that of the existing above-ground individuals (Nunney 2002). A persistent seed bank could also slow the rate of response to selective pressures, as only long-term environmental patterns affect the genetic composition of the seed bank as a whole (Levin 1990).

Seed banks also play an important role in population dynamics. A species' survival in a challenging environment is at least partially dependent on its having a persistent seed bank, which can survive in the soil for many generations (Cohen 1966). Having a seed bank reduces a species' risk of local extinction, as holding seeds in the soil that can germinate in later years reduces the impact of years with minimal seed production and spreads mortality risks out over time (Levin 1990).

The soil seed bank could impact community composition by serving as a reservoir for species not currently present in the above-ground layer. In the event of atypical environmental conditions, usually associated with disturbance (such as prolonged draw-down in a marsh, or an opening of the forest canopy by a treefall gap), germination from the seed bank can cause shifts in the above-ground vegetation composition (Wilson *et al*. 1993). Because the soil seed bank has the potential to strongly influence community composition, especially during times of environmental fluctuation or disturbance, it is an important component of the forest to consider when thinking about the effects of a disturbance on an area.

Effects of forest management treatments

In many eastern deciduous forests, managers have used forest thinning and fire to introduce disturbance for a variety of reasons, ranging from restoration of hypothesized prior conditions to encourage oak regeneration, to management for specific habitats (Brose *et al*. 2001). These common forest management techniques are some of the primary anthropogenic disturbances in eastern deciduous forests (Whelan 1995, Brose *et al.* 2001). These disturbances have been shown to alter the species composition of above-ground vegetation, increasing graminoids, summer forbs, and seed-banking species (Hutchinson *et al*. 2005). However, few studies have examined the effects of these treatments on the soil seed bank in the eastern deciduous forest.

Consideration of the known effects of disturbances can help to form hypotheses about what effects such disturbances might have on the soil seed bank. Thinning removes trees, opening up the canopy and allowing more light to penetrate to the forest floor. Increased light levels may increase germination of seeds from the soil seed bank (Pons 1992). Burning removes leaf litter from the forest floor as it is consumed in the fire, and leaves a layer of ash on the ground. These effects simultaneously allow more light to penetrate to the soil and darken the soil. Litter removal allows soils to absorb more light, and consequently warm more, which may increase germination (Auld and Bradstock 1996). However, as the canopy remains in place, sunlight reaching the soil is still filtered through the canopy. Heat from fire may also kill seeds that are susceptible to heat damage (Baskin and Baskin 1998). As fires in eastern deciduous forests tend to be cooler than those in some other systems, heat effects may be less important in eastern forests. Temperatures from fire also drop off fairly quickly in the soil, so that while surface temperatures may be hot enough to kill seeds, such high temperatures may only penetrate ~1 cm into the soil (Chaplick and Quinn 1988). Seeds buried deeper than 1 cm would then not be exposed to dangerously high temperatures. A combination of fire and thinning removes both the leaf litter and a portion of the canopy, potentially providing a greater level of light and soil warming then either practice alone. If some seeds germinate in response to light or heat above a threshold (Hill and French 2003), this combination of treatments may allow them to germinate when one treatment alone would not.

While the effects of forest treatments on the soil seed bank have not been well-studied in eastern deciduous forests, studies on the effects of management treatments and other disturbances on the seed bank have been conducted in other ecosystems. Studies in a variety of fire-prone or fire-dependent ecosystems have revealed differing effects of fire on seeds, killing some (Watkinson *et al.* 1989, Meney *et al.* 1994), breaking dormancy and/or increasing germination in others (Hill and French 2003), and having no effect on still others (Manders 1990, Odgers 1996). Hill and French (2003) reported a range of seed responses from one site. Ferrandis *et al*. (2001) noted that characteristics of a fire (intensity and frequency) will influence the effects on seeds in the soil. Thus, specific conditions at the time of a fire will largely determine the effects on the seed bank. Less intense fires will have less of an impact on seeds in the soil, while intense fires which heat the soil for longer duration or to greater depths will have a greater impact on seeds in the soil, likely killing more seeds. The wide range of possible effects from disturbance make it difficult to predict the potential impacts on the soil seed bank. Clearly, explicit study of the impacts of these management treatments is necessary.

Spatial heterogeneity

Just as pattern is observed in the arrangement of plants on the landscape, pattern is found in the spatial arrangement of seeds in the soil. Spatial heterogeneity – the tendency of things to be unevenly distributed in space (Dutilleul 1993) – is of critical importance to population dynamics in forested ecosystems. Coarse-scale heterogeneity can result from environmental factors such as large-scale disturbances, slope, or moisture gradients. Medium- to fine-scale heterogeneity may result from physical variability or microtopography. For example, differences in slope or small depressions in the ground can affect how seeds or leaf litter move across the ground surface and where they tend to collect. Population processes such as treefall gaps or the seed dispersal area around an individual plant or seed head can also produce fine-scale heterogeneity. Both physical and biological processes may take place on a broad or fine scale (Legendre and Legendre 1998).

Studies of soil seed banks have revealed spatial heterogeneity at many scales (Major and Pyott 1966, Thompson 1986, Benoit *et al*. 1989, Matlack and Good 1990, Dessaint *et al*. 1991, Olano *et al*. 2002). Seed dispersal patterns are one reason for fine-scale heterogeneity. As seeds are produced and dispersed, they tend to be more or less concentrated around the parent plant (Harper 1977). The movement and deposition of seeds across the landscape is also dependent on spatially heterogeneous factors, such as roughness of the soil surface, surface depressions, and the presence of bird roosts (Silvertown and Lovett-Doust 1993, Russell and Schupp 1998). Large-scale disturbances, such as forest management, can impact heterogeneity at many scales by creating coarse-scale heterogeneity across the landscape, while also driving finer scales of heterogeneity through their impacts on canopy cover and other environmental variables, or on population processes (Walters and Stiles 1996, Brosofske *et al*. 2001). Patterns of spatial heterogeneity in oak forests are not well understood, in either the understory or the soil seed bank. If we are to study these forests, it is important to understand the plant-relevant scales of variation and to base our studies on such scales (Wiens 1989).

The objectives of this study were to examine the soil seed bank of areas subjected to forest management regimes and assess any differences between them, and to assess the spatial pattern of the soil seed bank at fine scales. In particular, this research addresses three main questions: 1) Does composition of the soil seed bank vary among forest management treatments? 2) Does the soil seed bank species composition differ from the above-ground species composition within treatments? 3) What is the spatial structure of the soil seed bank at fine scales, and how does it relate to typical forest management treatments?

Methods

Site description

The study sites were located in Vinton County, Ohio, with one replicate at Zaleski State Forest (39°35’5”N 82°37’0”W) and one at Vinton Furnace Experimental Forest (39°20’0”N 82°39’0”W) in the Raccoon Ecological Management Area (REMA; Figure 1). Both sites are located in southeastern Ohio, in the Low Hills Belt of the Unglaciated Allegheny Plateau, which is located within the Mixed Mesophytic Forest Region (Braun 1950). This area is characterized by deeply dissected topography, with low hills and valleys with moist bottoms (Braun 1950). The underlying bedrock is primarily sandstone, overlain by shale (Forsyth 1970). The vegetation consists of mixed oak forest, with *Quercus* spp. and *Carya* spp. as typical forest dominants on the ridgetops, and *Acer saccharum* and *Liriodendron tulipifera* more prevalent in the valleys (Braun 1950). The herbaceous layer consists of both herbaceous and woody species, and is highly species-rich, as is common in eastern deciduous forests (Small and McCarthy 2002*b*, Gilliam and Roberts 2003, McCarthy 2003). The average annual temperature is 11.3 °C, with average annual precipitation of 1024 mm (Hutchinson *et al*. 2005). The forests of this area were clearcut to produce charcoal for local iron furnaces in the mid to late 1800’s, but were not cleared for row-cropping (Braun 1950, Hutchinson *et al*. 2005).

Experimental treatments

The study sites are part of the Ohio Hills unit of the USDA Forest Service's Fire and Fire Surrogate (FFS) study (Yaussy 2001). The FFS Study was designed to investigate the effects of forest management treatments (specifically, thinning and burning) on various aspects of forest functioning. The experimental sites are set up in a randomized complete block design, with four ± 20 ha units in each forest replicate. Each unit was subjected to a different forest management regime: burning, thinning, thinning followed by burning, and an untreated control area (Yaussy 2001). All thinning was conducted in Fall-Winter 2000-2001, and all burns were conducted in Spring 2001 (Yaussy 2001). Thinned areas were commercially thinned from below to ~13.75 $m^2 \cdot ha^{-1}$ of basal area (Yaussy 2001). Burning was introduced to restore what are believed to be historical ecosystem processes by returning frequent, low-intensity fires to the area (Brose *et al*. 2001). Thinning was introduced to restore what is believed to be historical ecosystem structure; i.e., density and spatial pattern of trees (Yaussy 2001).

Field methods

Experiment 1

Ten 20 × 50 m permanent plots were established in each treatment unit (Figure 2). Each 20 × 50 m plot was divided into ten 10 × 10 m subplots. Circular 1 m^2 vegetation plots were placed in one or two corners of each of these subplots (Figure 3). These were sampled once in the summer of 2004, generating the above-ground data used in this study

(T. F. Hutchinson, unpublished data). Soil samples were taken immediately outside the vegetation plots located in four of the ten subplots in each 20 × 50 m plot. The leaf litter layer was removed and a 10 × 10 × 5 cm soil sample was collected from the mineral and organic soil. These soil samples were combined to produce one 1000 cm^3 combined sample for each subplot. Four such combined soil samples represent each 20 × 50 m plot ($N = 320$). The soil samples were collected March 13-28, 2004. Collection of samples in the early spring allowed for natural cold-stratification over the winter, thus breaking some seed dormancy (Schiffman and Johnson 1992, Thompson *et al.* 1997, Bossuyt *et al.* 2002).

Experiment 2

Two parallel 20 m transects were laid 50 m apart in both the Control and Thin & Burn units at Zaleski State Forest. Transects were run perpendicular to the slope (along the contour) to avoid picking up possible effects of elevation or moisture gradients. A 10 × 10 × 5 cm soil sample was collected every 0.5 m along the transects, for 40 samples per transect. Leaf litter was removed, and the organic and mineral soil layers were collected. Soil samples were collected March 14-15, 2005.

Micro-environmental data (canopy cover, leaf litter depth (cm), and percent cover of bare ground and leaf litter) were collected at each sampling point (40 per transect). Canopy cover was scored on a 1 - 4 scale, with 1 = 0-25% cover, 2 = 26-50%, 3 = 51-75% and 4 = 76-100%. As percent cover of bare ground was 0 across all transects and treatments, and percent cover of leaf litter was 100 across all transects and treatments, no further analysis was performed on these data.

Greenhouse procedures

Soil samples were collected in Ziploc bags and stored in the cold room at approximately 4 °C until all were collected. Soil from each subplot was then sieved and examined to remove any insects, roots (large enough to resprout), stones, and other plant matter, and spread in a 19.8 × 19.8 × 4.5 cm square aluminum foil cake pan over a 1 cm layer of fine vermiculite. A paper napkin was placed in the bottom of each pan to prevent escape of the vermiculite, and thirteen pinholes, evenly spaced, were pricked in the bottom of each pan to allow for drainage,.

The pans were placed in the greenhouse, with a 16-hour day, 8-hour night light regime. Temperatures were approximately 25 °C during the day and 15 °C at night. Pans were watered as needed, approximately every other day. Pan location was randomized regularly (approximately once every two weeks) to reduce any effects from microclimatic variations within the greenhouse. Germination was monitored and recorded, and seedlings were marked and identified as soon as possible. Seedlings that could not be identified were grown until such time as they could be identified. Botanical nomenclature follows Gleason and Cronquist (1991). To detect possible contamination by seeds of greenhouse weeds, pans with greenhouse potting mixture were placed among the sample pans. No greenhouse weeds were detected in this way.

The use of this emergence method is widely practiced (Gross 1990, Brown 1992). Its main drawback is the potential failure to detect seeds which do not have their dormancy broken or germination conditions met by the conditions provided (in this case, cold-stratification, followed by regular regimes of light and watering). Thus, the species list produced here is a minimal estimate of the composition of the soil seed bank. While both the emergence and flotation/inspection methods have their advantages and disadvantages, the two methods have been reported to perform with equal accuracy in the assessment of species composition, relative abundances of species in the seed bank, and differences between treatments or areas (Ball and Miller 1989, Brown 1992). Schneider and Sharitz (1986) found many more seeds by sieving than by germination – however, when tested for viability, the sieving results agreed with the germination results. Some have suggested that a combination of emergence and visual inspection is best for optimal detection of seeds and a more accurate representation of the soil seed bank, as the use of either method alone is likely to lead to an underestimation of the seed bank (Schneider and Sharitz 1986, Ishikawa-Goto and Tsuyuaki 2004).

Considering these recommendations, a subsample of pans from Experiment 1 was selected following assessment of the seed bank composition by the emergence method and visually inspected with the aid of a dissecting microscope to determine if any ungerminated viable seeds remained in the soil. Two pans were randomly selected to represent each treatment unit and forest replicate combination, for a total of 16 samples. After drying and thorough mixing, a 50 mL subsample was drawn from each of the 16 pans and passed through a series of sieves (2.00, 1.40, 1.00, and 0.25 mm). Each fraction was then visually examined with a dissecting microscope. This provided a volume of soil and percentage of total plots and sites examined that was comparable to those used in previous studies that used visual inspection following emergence (Moore and Wein 1977, Matlack and Good 1990, Schiffman and Johnson 1992). This subsampling was not intended to provide quantitative data, but rather to assess the efficacy of the emergence method in this forest type, and to determine if some species in the soil seed bank were undetected by the emergence method.

Analytical methods

Experiment 1

Species richness (*S*) of the soil seed bank was compared across the four forest management treatments, and the species richness of the above-ground vegetation was compared with that of the soil seed bank within each treatment. The Shannon-Weiner diversity index (α diversity) was calculated for each treatment area ($H' = -\Sigma\, p_i \ln p_i$; Shannon and Weaver 1949). The mean species richness and mean Shannon-Weiner diversity index, and standard errors for each, were also calculated for each treatment. These values were compared with an ANOVA, using Number Cruncher Statistical Systems (NCSS; Hintze 2001).

Sørensen's distance measure was applied to the presence-absence data from the soil seed bank, and the similarity between the soil seed bank composition in the various treatment areas was assessed with cluster analysis using PC-ORD (McCune and Medford 1999). This method was also used to assess the similarity between above-ground and seed bank species composition. In both cases, the flexible beta linkage method was used ($\beta = -0.25$). This combination of distance measure and linkage method was chosen because 1) the Sørensen distance measure and flexible beta linkage method are compatible, 2) the flexible beta linkage method with β = -0.25 is space-conserving, and therefore performs well while reducing distortion, and 3) this combination of distance and linkage methods minimizes chaining (McCune and Grace 2002). The use of other distance measures or linkage methods (farthest neighbor and group average) did not change the structure of clustering.

A multiple response permutation procedure (MRPP) was also performed using PC-ORD (McCune and Medford 1999). This nonparametric procedure tests the hypothesis of no difference between two or more groups (McCune and Grace 2002). Sørensen's distance was used. Comparisons were made between each possible pairwise combination of treatment groups. All groups were the same size, consisting of 20 plots. An MRPP was also performed to compare the species composition of the soil seed bank and above-ground vegetation in each treatment area. Again, each group contained 20 plots.

A principal coordinates analysis (PCO) was conducted using Multi-Variate Statistical Package, Version 3.00 (MVSP) (Kovach 1998). This procedure uses a similarity or distance measure to place plots in multi-dimensional species space, such that plots with more similar composition are located closer to one another, and plots with greater compositional differences are placed further apart (Legendre and Legendre 1998).

To explore whether differences in composition between the treatments might be more visible in functional group classes, the species were divided into six functional groups: annual forbs, perennial forbs, other forbs (forbs that were not identified or classified as annual or perennial), graminoids, shrubs and lianas, and trees. These six functional groups were included in a loglinear model, which examines the relationships between variables (Hintze 2001). Interactions between site, treatment, and functional group were examined using a loglinear model generated using NCSS (Hintze 2001). Site, treatment, and functional groups were defined as the three factors, and a full model was generated using the step-down method. A subsequent breakdown of each interaction was conducted by generating a table of interactions to analyze the percentages of the factors in each term of interest (Hintze 2001).

Experiment 2

Spatial autocorrelation was used to assess species and environment data. The most commonly used measure of spatial autocorrelation in ecological studies is Moran's I (Moran 1950). This measure essentially provides a single value that summarizes the degree of correlation between two data sets at a given distance of separation. It is analogous to Pearson's correlation coefficient, r (Legendre and Legendre 1998).

Assessment of spatial autocorrelation (Moran's I) was conducted using GS+ (Gamma Design Software 2004). Spatial autocorrelation values were calculated based on species richness (S) and Principal Coordinates analysis (PCO) scores. PCO scores provided a single value that represented the unique species composition of each sample and was appropriate to enter into spatial assessment software. Micro-environmental data (canopy cover and litter depth) were also analyzed using GS+ software to assess spatial autocorrelation. Statistical significance of Moran's I values was tested for every distance class with a Monte Carlo randomization approach using 1000 permutations. Monte Carlo randomization was performed using Rookcase software (Sawada 1999).

Results

Experiment 1

Soil seed bank effects

A total of 70 taxa were recorded across all treatments. Forty-five taxa were identified to species level, 9 taxa were identified to genus, 2 were identified to family, and an additional 14 taxa were recognized as morphologically distinct but not identifiable to taxon – all will hereafter be referred to as "species" (Table 1). Of these taxa, there were 9 annual forbs, 23 perennial forbs, 12 forbs that could not be identified as annual or perennial (44 total forbs), 20 graminoids, 4 shrubs/lianas, and 2 trees (Figure 4). Only three identified species were not native (*Digitaria ischaemum*, *Polygonum convolvulus*, and *Verbascum thapsus*), and none were frequently found. An individual of *Typha* was not identified to species; if *Typha angustifolia*, the total number of non-native species would then be four.

Species richness (*S*) was determined for each treatment unit, both for each forest replicate and for both sites combined (Figure 5). In combined totals, the Thin & Burn unit had the greatest number of species, and the Thin unit contained the fewest (Table 2). The mean species richness was not significantly different ($P < 0.05$) among the treatments. The Shannon-Weiner diversity index (H') was calculated for each treatment unit. Mean Shannon-Weiner index values were not significantly different ($P < 0.05$) among the treatments. Visual inspection of the soil at the conclusion of the emergence period revealed seeds of only three species, occurring at low numbers (0-16 seeds per sample) across the treatments. Thus, the emergence method appears to have effectively captured the species composition present in the soil seed bank of these sites.

Species composition of the forest management treatment units was not distinct, as revealed by a cluster analysis (Figure 6). A multiple response permutation procedure (MRPP) showed largely the same result. Most pairs of treatment groups were not significantly different, but the Control and Thin & Burn units were significantly different from one another (T = -1.868, P = 0.0497; Table 3a). The relatively small magnitude of the test statistic (T) values indicates that the groups are weakly separated. Low chance-corrected within-group agreement (A) values are common for community data. The overall comparison (an analysis of all treatments) showed no significant difference between the groups (T = -0.935, P = 0.1609). The above-ground vegetation also appears to be fairly consistent among treatments, with some of the more frequently found species occurring in all treatment units.

Separate analysis of the two forest replicate blocks essentially confirmed the results obtained by the combined analysis (Tables 3b and 3c). No overall patterns of treatment differences emerged, though differences between treatments were found within sites. In Zaleski, the Thin & Burn unit was significantly different from both the Thin unit and the Burn unit. In REMA, the Control unit was significantly different from the Thin unit and the Burn unit. Additionally, the Thin & Burn unit was significantly different from the Thin unit. These differences between sites indicate a treatment by site interaction. Such differences could be based in existing biological differences between the treatment units at a given site.

While a combined analysis showed no significance between treatments, separate analyses showed inconsistently significant results. Those treatment pairs which show significant differences at one site are not significant at the other. The one exception to this is in the comparison of the Thin and Thin & Burn units, which is significant at both sites. Other than this one pairwise comparison, no distinct differences between treatments are apparent at both sites. The inconsistency of these results creates some difficulty in interpretation. While it is possible that these differences are the result of treatment effects, it is equally possible that results found in only one of two forests are the result of individual site idiosyncrasies and not treatment effects. Without trends which appear in both forest blocks, it seems that the results found from the combined analysis (that is, no clear differences in composition between treatment units) hold.

The lack of clear differences in species composition between the treatments was also apparent in the principal coordinates analysis (PCO). Here we see all four treatments overlapping, with no clear trend of separation (Figure 7). One group of plots did fall out separately from all the others – those belonging to the REMA Thin & Burn unit. This unit appears to be compositionally different from not only the other treatments, but also from the Zaleski Thin & Burn unit. PCO revealed that the REMA Thin & Burn unit is floristically unique, and thus a poor replicate of the Zaleski Thin & Burn unit.

Soil seed bank vs. above-ground vegetation

Above-ground vegetation and soil seed bank composition were distinct, as shown by a cluster analysis (Figure 8). All above-ground vegetation plots separated into one

cluster, and all the soil seed bank plots grouped in a separate cluster; thus, composition was drastically different between the two strata. A significant difference between the above-ground vegetation and the soil seed bank within each treatment area, as well as overall ($T = -95.273$, $P < 0.0001$) was also found by MRPP analysis (Table 4a). The large magnitude of these T values indicates that there is very strong separation between the seed bank and the above-ground vegetation in each treatment. The values of A ($A = 0.187 – 0.225$) are within the expected range for community data ($A < 0.3$)
Similar results were found when the same data were analyzed for each forest replicate separately (Tables 4b and 4c). Because factors cannot be nested in an MRPP, separate analyses and tables were generated for each forest to allow site differences to be explicitly examined. As the results were the same (composition of the soil seed bank and above-ground vegetation were significantly different in all treatments), no site difference was found.

The above-ground vegetation was found to contain 253 species (T. F. Hutchinson, unpublished data), and 70 species were found in the seed bank. If unknown species are excluded, that leaves 244 species in the above-ground vegetation and 56 species in the soil seed bank. Of those, 36 species are held in common. This means that 51.4% (64.3% of identified species) of species in the soil seed bank were found in the above-ground vegetation, but only 14.2% (14.8% of identified species) of above-ground species held seed in the soil seed bank.

Functional group analysis

Over half of the soil seed bank was composed of forbs, with graminoids also prominent, but few trees and shrubs (Figure 9). Examination of functional groups using loglinear analysis revealed variation within the “functional group” class, due to large differences between the proportion of tree species and herb species, but no significant treatment by functional group effect (Table 5). A breakdown of the site by treatment interaction indicated that the significance of this interaction is primarily driven by the floristically unique REMA Thin & Burn site. Because the treatment by functional group interaction was close to significant ($P = 0.087$), it was broken down to assess which terms were important. This breakdown indicated an increase in graminoids in the Burn unit, a smaller percentage of perennial forbs in the Control plot than in the treatments, and shrubs and trees both having their greatest frequency in plots in the Control areas (Figure 10).

Experiment 2

Soil seed bank

Species richness exhibited no consistent spatial pattern in either the Control or Thin & Burn unit (Figure 11). In the Control unit, community composition (represented by PCO scores) had no spatial pattern on the scale examined (0-20 m). In the Thin & Burn unit, community composition was significantly spatially autocorrelated along one of the two transects. On that transect, significant positive autocorrelation was discovered at distances of 0.5–4.0 m, and significant negative autocorrelation was found at distances from 10.0–13.5 m (Figure 12). The differences in spatial patterning between the two transects in the Thin & Burn unit indicate a patchy treatment effect or other variability in spatial ordering on the scale of 50 m.

Environmental variables

Environmental variables were assessed for spatial autocorrelation. Canopy cover was spatially autocorrelated in the Thin & Burn treatment, with significantly positive autocorrelation from 0.5 to 2.0 m and significant negative autocorrelation from 5.0 to 10.0 m on one transect, and 8.5 to 10.0 m on the other. This scale of autocorrelation is close to that found for species composition in the Thin & Burn unit, suggesting that canopy cover may drive or contribute to spatial variation in species composition at a fine scale. By contrast, the canopy cover in the Control unit was spatially autocorrelated only from 0.5 to 1.0 m – at very fine scale (Figure 13). Again, this lack of spatial organization in the canopy cover matches the lack of spatial organization in the species richness and composition of the soil seed bank in the Control unit. Litter depth was not spatially autocorrelated at any lag distance over a 20 m scale. This absence of spatial patterning in litter depth was found in both the Control and Thin & Burn units (Figure 14).

Discussion

Three years following forest management treatments, the species composition of the soil seed bank of treated areas was not strongly altered relative to the Control, though some functional groups do appear to have shifted in prevalence. This indicates that thinning and burning do not produce a wholesale change in the species composition of the soil seed bank in the short-term (three years following one fire). While studies of above-ground vegetation have shown a shift in species composition following fire (Nuzzo *et al*. 1996, Arthur *et al*. 1998, Hutchinson *et al*. 2005), this effect tends to come about as a result of germination out of the soil seed bank. Thus, while the species richness above-ground may increase, there is not a corresponding increase in species richness of the seed bank. However, germination out of the soil seed bank does not necessarily result in a net decrease of seed in the seed bank. As species germinate out of the soil seed bank and the plants flower and drop seed back to the ground, the seed bank is recharged with younger, fresher seeds.

The only significant difference in the overall composition of the soil seed bank was found between the Control and Thin & Burn treatments. One would expect the Thin & Burn unit to be the most disturbed, as it was subjected to two forces of disturbance. Thus, the greatest effects might be expected in this group. A shift in species composition of the soil seed bank to more early successional species may be expected following disturbance if those species germinate out of the seed bank (or disperse into the area) and are growing well in these more open disturbed conditions, and dropping seed. However, my findings indicate that, on a broad scale, the seed banks of these forests are relatively uniform in composition, regardless of treatment. Though other differences in species composition were found between treatments at single sites, the lack of a pattern across both sites makes these results difficult to interpret.

This apparent lack of strong difference between the treatment units is also found by the Principal Coordinates Analysis (PCO). The PCO also shows no strong separations based on site. Though the plots from the Thin & Burn unit of REMA form a separate group in the plot of the first two PCO axes, no other groups of plots form such a cluster of points. The separation of this group of points indicates a distinct species composition. However, the REMA Thin & Burn unit is both floristically and topographically somewhat different from the other units. This is likely the driving force behind its separation from the other units.

Contrasts in species composition between above-ground vegetation and the soil seed bank have been widely reported in the literature from many forest types, including pine and hardwood forests, and old-growth and second-growth forests (Scheiner 1988, Schiffman and Johnson 1992, Bossuyt *et al*. 2002, Decocq *et al*. 2004, Leary and Howes-Keiffer 2004). Here, I found that 51% of species occurring in the soil seed bank were also found above-ground, but only 14% of species in the above-ground vegetation were found in the soil seed bank. This is largely due to the fact that many of the above-ground species are woodland herbs, which do not generally maintain a persistent soil seed bank (Leckie *et al*. 2000). Bossuyt *et al*. (2002) report that in Belgian forests of varying age, the species most frequently found in the above-ground vegetation are absent in the soil seed bank and vice versa. My findings are quite the opposite – nine of the ten most frequent species in the soil seed bank were found in the above-ground vegetation, both in the control and the treated units. Thus, it is unlikely that disturbance in these areas would result in a widespread change to the above-ground vegetation due to germination from the seed bank. Other studies in managed deciduous forests (oak and pine-hardwood) have also found species in common between the two strata (Scheiner 1988, Decocq *et al*. 2004). Pickett and McDonnell (1989) note that disturbance regimes will not necessarily cause a complete change in the species composition of the soil seed bank of an area, though such disturbance may create a shift in the composition and size of the seed bank, especially if the anthropogenic disturbances are more intense or more frequent than the natural regime.

Several common seed bank species are prevalent in the above-ground vegetation following disturbance, including *Carex* spp., *Rubus* spp., *Erechtites hieraciifolia*, and *Liriodendron tulipifera*. The majority of the species that are frequent above-ground but not found in the soil seed bank are tree and shrub species (seedlings of canopy and subcanopy species such as *Carya* spp., *Quercus* spp., *Nyssa sylvatica*, *Sassafras albidum*, and shrubs or vines such as *Smilax* spp., *Viburnum acerifolium*, *Toxicodendron radicans*, and *Vaccinium* spp.). Studies of other forest types have found very few tree species or forest herbs maintaining a soil seed bank, with early successional or ruderal species comprising the majority of the soil seed bank (Pickett and McDonnell 1989). My findings agreed with these studies in part, with only two tree species, and four shrub (woody) species in the seed bank. The two tree species – *Acer rubrum* and *Liriodendron tulipifera* – are widespread in the understory layer of these forests, as are some shrub species, including *Rubus* spp. and *Vitis* spp. Though species of disturbed habitats were common in the seed bank, old field species were not, which agrees with results from other second-growth forests on land that was never agricultural (Scheiner 1988, Schiffman and Johnson 1992). Colonizing species with wide ecological amplitude, such as species of *Rubus*, *Carex*, and *Juncus*, which commonly occurred in my plots, are found in seed banks throughout the northern temperate region, often in great densities (Oosting and Humphreys 1940, Marquis 1975, Moore and Wein 1977, Decocq *et al*. 2004).

Disturbance of this ecosystem via thinning and prescribed fire influenced the relative dominance of functional groups in the soil seed bank. Though the interaction of treatments and functional group was not statistically significant, general trends in the frequency of functional groups can be described. For instance, the relative frequency of graminoids was increased in areas that experienced only prescribed fire. This shift is consistent with other studies that have demonstrated a relationship between fire frequency and increased incidence of graminoids (Hutchinson *et al*. 2005). Treatment plots exhibited increased relative frequency of perennial forbs in the seed bank relative to the Control. This increase may be due to the fact that forest understory forbs are often light-limited and operate with a tight energy budget (Muller 1978). Thus, flowering and seed production may be limited under the closed canopy of the Control unit relative to treatment units, where light availability has been enhanced. In contrast, shrubs and trees were both most numerous in the Control areas. This reduction of woody species in the soil seed bank may occur if species germinate out of the seed bank under conditions of greater light availability but do not produce seeds to replenish the soil seed bank.

At broad scales, species diversity and composition showed no significant difference among forest management treatments. However, fine-scale spatial patterns in species composition and environmental factors differed between the Control and Thin & Burn units. Thus, the scale of comparison can alter the patterns observed.

Different patterns of fine-scale spatial organization emerged in disturbed and undisturbed forests. Differences were apparent both in biological variables (species composition) and physical variables (canopy cover). The Control area exhibits no spatial ordering on the scale of 0-20 m. By contrast, significant spatial ordering was detected in the Thin & Burn unit, in both species composition and canopy cover.

Species richness had no consistent spatial pattern in either the Control or Thin & Burn units. Community composition followed different spatial patterns in the two treatment units. Again, no spatial pattern was found in the Control unit, but spatial autocorrelation was found in the Thin & Burn unit. In the Thin & Burn unit, plots were more similar when located within 4 m of one another. This seems to represent a clustering of species at the scale of a single tree canopy or canopy gap. The spatial range of seed dispersal around a parent plant is also included within this distance. Suzuki *et al.*'s (2005) study of *Lysimachia rubida*, a biennial forb that does not reproduce asexually, found clustering of first-year plants around reproductive individuals on the scale of 0.4-2.4 m. This distance would fall within the 4 m range of similar species composition found in the Thin & Burn unit here. Thus, short-range seed dispersal may be one factor that helps to structure the clustering of similar species under a canopy or gap. In the Control unit, species grow somewhat randomly. In the Thin & Burn unit, canopy gaps introduce spatial structuring by encouraging the growth and flowering of certain light-responsive species. These species may then perpetuate themselves in a cluster, driven by short-distance seed dispersal and the light conditions that encouraged their growth initially.

Distinct patches or clusters with significantly different species composition were found in plots 10-13.5 m apart. This scale appears to represent a transition from a tree canopy into a canopy gap, or vice versa. This distance closely matches documented diameters of canopy gaps in northern hardwood forest (Mladenoff 1990). However, this spatial pattern was found on only one of the two transects in the Thin & Burn unit. Thus, the spatial pattern also varies over a scale of 50 m. This indicates that spatial pattern of species composition is patchy at various scales.

The spatial pattern of canopy cover closely matched that of the species composition in both treatments. This suggests that canopy cover and gaps contribute to, and may be important drivers of, variability in species composition of the seed bank. Compositional differences in understory vegetation have been found to be highly correlated with differences in canopy cover (Brosofske *et al*. 2001). In the Thin & Burn unit, canopy cover was similar over short distances (0-2 m), and different at scales of 8-10 m. This spatial pattern closely matches that of species composition in the Thin & Burn unit. Both transects in the Thin & Burn unit show this canopy pattern, but only one shows autocorrelation of species composition. Differences in spatial pattern of composition are likely due to an interaction of environmental factors, such as canopy gap, and other factors that are spatially dependent, such as seed dispersal, ability of seeds to get to the site, and patchy burn effects (Silvertown and Lovett-Doust 1993). While canopy gaps appear to be an important structuring force, species composition of the seed bank is still fundamentally dictated by the seeds that can disperse into an area. In the Control unit, a lack of spatial organization in the canopy cover corresponds with a lack of spatial patterning in the species composition. The spatial autocorrelation of canopy cover in the Control unit is restricted to a very fine scale (0–1 m), which likely corresponds to a gap in the branches of the intact canopy. These small gaps do not appear to affect the outcome that I detected in the species composition in the Control unit.

An absence of spatial patterning in litter depth was found in both the Control and Thin & Burn units. This result differs from that of Ferrari (1999), who found quantities of leaf litterfall to be spatially correlated with the position of trees. However, Ferrari was working on a somewhat larger scale (140 × 360 m), and examined the mass of leaf litter, and considered leaf litter of individual species separately. The overall spatial pattern of leaf litter or depth of litter may behave differently. The patterns of leaf litterfall of single trees or species may be obscured by overlapping leaf litter “footprints.” Measurements of leaf litter mass by species and overall leaf litter depth also may not be well correlated, particularly if different species have leaf litter with different properties. Leaf litter can move over the landscape, and may do so in ways that are not spatially dependent. The movement of leaf litter may also occur at scales that are larger than the scale of my transects (as Ferrari’s (1999) findings would suggest) or are otherwise not detectable at fine scales.

When considering the soil seed bank, the main factors that impact its composition are those that control the dispersal of seeds into the site, including seed production by plants in the above-ground layer, the primary dispersal patterns of those seeds, and secondary seed dispersal. Patchy seed mortality or germination may also impact patterns of composition in the soil seed bank. Seeds will aggregate around the parent plant, so that many of the seeds produced in an area will likely remain there, close to the parent (Howe 1989). This dispersal pattern suggests that any management effects on the above-ground vegetation may also permeate into the soil seed bank immediately below. For example, *Impatiens capensis* has been found to have greater floral density and greater seed production under canopy gaps (Walters and Stiles 1996). Much of this increased seed production will remain relatively close to the parent plant. Thus, management practices that open up the canopy may increase flowering in some species, and thereby increase those species' inputs into the local seed bank.

A key component of disturbance or forest management treatments is the patchy nature of these disturbances. Patchy effects of management (both environmental and biological) have serious implications for management plans and monitoring. Forest management appears to generate patchy biological changes, which may not be apparent at broad scales, but which are detectable at fine scales. At broad scales, physical processes (such as canopy gaps, etc) can dominate biological effects. However, local biological interactions can create webs of indirect effects which modify the direct effects of physical patterns (Wiens 1989). At the fine, plant-relevant scales, changes in environmental (physical) conditions are detectable. These changes will generate population dynamics effects, which will in turn impact the community dynamics.

While it is widely acknowledged that fires burn in a patchy manner (Price *et al.* 2003), and that thinning or removal of trees will necessarily result in a patchy mosaic, these spatially patchy effects are generally not explicitly addressed in forest management plans or when studies of the effects of management are being carried out (Wiens 1989). The effects of these treatments may occur on a finer scale than is typically studied in monitoring efforts. This may result in a failure to detect plant-level effects of such treatments. Here, I have looked specifically at impacts on the soil seed bank, which can play a critical role in population and community dynamics. The implications for management and monitoring are that one must either sample at multiple scales to effectively sample an area or seriously consider the relevant scales before sampling.

Conclusion

Single burning or thinning events do not cause a significant change in the species composition or diversity of the soil seed bank of second-growth forest that was never plowed for agriculture. Species composition of the soil seed bank and above-ground vegetation are quite different, as reflected in much greater above-ground species richness. This is as expected, as forest forbs and woody plants often do not maintain a persistent soil seed bank. Though treatment effects on the soil seed bank may be visible immediately, any such effects are transient in nature and no longer visible three years after treatment. It is possible that more frequent or more intense treatments would yield a longer-term shift in composition of the seed bank. The possibility also remains that the effects of management treatments take longer than three years to accrue into the soil seed bank. However, as increased light availability resulting from treatments should tend to increase flowering and reproduction, it is unlikely that treatment effects from a single disturbance event would take many years to accrue into the seed bank.

The results from my first experiment showed no clear broad-scale effects of thinning and/or burning on the composition or species richness of the soil seed bank. However, there do appear to be fine-scale (on the order of 0-10 m) differences in community composition and species richness, both between treatment areas and within treatment areas.

The lack of significant autocorrelation in either species richness or species composition in the Control treatment suggests that, in the absence of management treatments or other disturbance, there are no clear fine-scale spatial patterns of seed bank composition. This is not to overlook the effects of topographical position – these are, of course, an important source of spatial variability at large scales (Small and McCarthy 2002*b*). Here, however, we are interested in fine-scale spatial variation and impacts of management treatments on such variation. The clear differences in spatial autocorrelation of community composition between the two transects in the Thin & Burn unit suggest a pattern of patchiness on a variety of spatial scales. This patchiness of disturbance should be more fully explored in future studies, and should inform both plans for management and assessments of the impacts of management.

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Table 1. List of species found in the soil seed bank at Zaleski State Forest and Raccoon Ecological Management Area, Vinton County, Ohio.
A (v) following the species name indicates that species was also found in the above-ground vegetation. Values in the treatment columns indicate the number of plots species were found in (of 80 overall, and 20 per treatment). Group indicates functional group type: annual forb, AF; perennial forb, PF; other forb, F; graminoid, G; shrub/liana, S; tree, T.

	Total	**Burn**	**Control**	**Thin**	**Thin & Burn**	**Native**	**Group**
Erechtites hieraciifolia (v)	63	12	14	18	19	Y	AF
Carex sp. (*C. pensylvanica* or *C. muhlenbergii*) (v)	60	13	17	15	15	Y	G
Rubus sp. (*R. occidentalis* or *R. allegheniensis*) (v)	56	16	17	13	10	Y	S
Panicum dichotomum (v)	34	5	7	12	10	Y	G
Carex sp. Wide (*C. platyphylla* or *C. laxiculmis*) (v)	33	8	7	7	11	Y	G
Eupatorium rugosum (v)	30	8	8	7	7	Y	PF
Viola blanda (v)	29	5	6	7	11	Y	F
Panicum sp.	28	10	4	8	6		G
Juncus tenuis	25	7	5	3	10	Y	G
Liriodendron tulipifera (v)	19	2	8	5	4	Y	T
Panicum commutatum (v)	18	7	3	4	4	Y	G
*Asteraceae**	17	1	4	5	7		F
Oxalis stricta (v)	17	5	1	8	3	Y	PF
Potentilla sp. (*P. Canadensis* or *P. simplex*) (v)	17	3	4	2	8	Y	PF
Antennaria neglecta (v)	14	2	5	1	6	Y	PF
Hedyotis caerulea (v)	13	2	2	3	6	Y	PF
Phytolacca americana (v)	13	5	1	5	2	Y	PF
Pilea pumila (v)	12	3	5		4	Y	AF
Vitis sp. (*V. riparia* or *V. vulpina*) (v)	11	1	5	2	3	Y	S
unknown dicot 2	11	1	3	4	3		F
Galium triflorum (v)	10	3	1	3	3	Y	PF
Lysimachia quadrifolia (v)	9	3		2	4	Y	PF
Saxifragaceae (*Heuchera Americana* or *Tiarella cordifolia*) (v)	9	1	3	2	3	Y	F
Rhus glabra (v)	8	4	3		1	Y	S
Lobelia inflata	6		1	1	4	Y	PF
unknown grass 1	6		5	1			G
Acalypha virginica (v)	5	1		2	2	Y	AF
Arisaema triphyllum (v)	4	1			3	Y	PF
Conyza canadensis	4	2			2	Y	AF
Hypericum punctatum (v)	4	1		1	2	Y	PF
Rhus copallina (v)	4		2	1	1	Y	S
Verbascum thapsus	4				4	N	PF
unknown dicot 5	4	1		3			F
Amphicarpaea bracteata (v)	3			1	2	Y	AF
Anemonella thalictroides (v)	3	1	1		1	Y	PF
Chamaecrista nictitans	3	1	1		1	Y	AF
Hedeoma pulegioides (v)	3		1	1	1	Y	AF

Table 1: continued.

Juncus sp. 2	3		2		1	Y	G
Panicum boscii (v)	3		1	1	1	Y	G
unknown grass 3	3	1	1		1		G
Acer rubrum (v)	2			2		Y	T
Helianthus divaricatus (v)	2		1	1		Y	PF
Polygonum convolvulus (v)	2	2				N	F
Solidago caesia (v)	2	1		1		Y	PF
unknown dicot 4	2		2				F
unknown grass 6	2	1			1		G
Aster lanceolatus	1		1			Y	PF
Cunila origanoides (v)	1	1				Y	PF
Digitaria ischaemum	1				1	N	G
Lespedeza hirta (v)	1		1			Y	PF
Ludwigia alternifolia	1	1				Y	PF
Ludwigia palustris	1				1	Y	F
Muhlenbergia schreberi	1				1	Y	G
Plantago rugelii (v)	1	1				Y	PF
Polygonum punctatum (v)	1			1		Y	AF
Ranunculus sp.	1				1		F
Schizachyrium scoparium	1		1			Y	G
Sisyrinchium angustifolium	1				1	Y	PF
Solanum carolinense	1		1			Y	PF
Solanum nigrum	1			1		Y	AF
Typha sp. (*T. latifolia* or *T. angustifolia*)	1	1				Y/N	PF
*Viola villosa***	1	1				Y	F
unknown dicot 1	1				1		F
unknown dicot 3	1				1		F
unknown grass 2	1			1			G
unknown grass 4	1	1					G
unknown grass 5	1				1		G
unknown grass 7	1	1					G
unknown grass 8	1	1					G
unknown grass 9	1				1		G

* presumed to be one species
***Viola hirsutula* (Cooperrider 1995)

Table 2. Mean (± SE) species richness (*S*) and Shannon-Weiner diversity (*H′*) statistics for the seed bank from four treatment units located in Zaleski State Forest and Raccoon Ecological Management Area, Vinton County, Ohio.
"Pan" indicates mean value (± SE) per 20 × 50m plot, and "plot" indicates total value across all 20 plots in each treatment.

	S		*H′*	
	pan	plot	pan	plot
Control	7.90 (0.68)	38	1.89 (0.12)	3.11
Thin	7.75 (0.78)	37	1.86 (0.10	3.03
Thin and Burn	9.90 (0.91)	48	2.10 (0.10)	3.33
Burn	7.50 (0.74)	43	1.82 (0.11)	3.23
Overall		70		3.36

Table 3. Multiple response permutation procedure (MRPP) for soil seed bank species composition in four treatments.
Comparisons are made for: a) both forest replicates combined, b) Zaleski State Forest, and c) Raccoon Ecological Management Area. *P*-values for Zaleski and REMA have been Bonferroni corrected to account for multiple comparisons. δ_{obs} = observed weighted mean within-group distance, δ_{exp} = expected weighted mean within-group distance, *T* = test statistic, *A* = chance-corrected within-group agreement.

a.

	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control vs. Thin	0.661	0.668	-1.517	0.0785	0.010
Control vs. Thin & Burn	0.631	0.639	-1.868	0.0497	0.013
Control vs. Burn	0.661	0.668	-1.517	0.0785	0.010
Thin vs. Thin & Burn	0.622	0.628	-1.211	0.1176	0.009
Thin vs. Burn	0.652	0.657	-0.891	0.1756	0.006
Thin & Burn vs. Burn	0.661	0.668	-1.553	0.0762	0.011

b.

	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control vs. Thin	0.612	0.622	-1.092	0.2727	0.016
Control vs. Thin & Burn	0.588	0.596	-0.998	0.3090	0.013
Control vs. Burn	0.647	0.650	-0.382	0.6213	0.005
Thin vs. Thin & Burn	0.547	0.569	-2.636	0.0291	0.038
Thin vs. Burn	0.606	0.622	-1.812	0.1026	0.026
Thin & Burn vs. Burn	0.583	0.607	-2.678	0.0308	0.040

c.

	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control vs. Thin	0.578	0.612	-3.448	0.0124	0.055
Control vs. Thin & Burn	0.620	0.635	-1.597	0.1440	0.024
Control vs. Burn	0.646	0.675	-2.987	0.0158	0.044
Thin vs. Thin & Burn	0.629	0.666	-3.235	0.0173	0.056
Thin vs. Burn	0.655	0.658	-0.281	0.7040	0.005
Thin & Burn vs. Burn	0.697	0.715	-1.518	0.1611	0.026

Table 4. Multiple response permutation procedure (MRPP) comparing composition of above-ground vegetation and soil seed bank in each treatment.
Comparisons are made for: a) both forest replicates combined, b) Zaleski State Forest, and c) Raccoon Ecological Management Area. *P*-values for Zaleski and REMA have been Bonferroni corrected to account for multiple comparisons. The compositions are significantly different in all treatments ($P < 0.05$). δ_{obs} = observed weighted mean within-group distance, δ_{exp} = expected weighted mean within-group distance, T = test statistic, A = chance-corrected within-group agreement.

a.

	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control	0.609	0.761	-23.259	<0.0001	0.199
Thin	0.545	0.703	-23.992	<0.0001	0.225
Thin and Burn	0.577	0.720	-23.117	<0.0001	0.199
Burn	0.611	0.751	-22.595	<0.0001	0.187
Overall	0.597	0.736	-95.273	<0.0001	0.189

b.

	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control	0.605	0.766	-11.105	<0.0001	0.210
Thin	0.542	0.693	-11.352	<0.0001	0.218
Thin and Burn	0.468	0.654	-12.309	<0.0001	0.285
Burn	0.583	0.733	-10.854	<0.0001	0.204
Overall	0.570	0.718	-48.257	<0.0001	0.205

c.

	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control	0.576	0.745	-11.695	<0.0001	0.227
Thin	0.499	0.698	-11.844	<0.0001	0.285
Thin and Burn	0.613	0.751	-10.412	<0.0001	0.184
Burn	0.612	0.759	-10.925	<0.0001	0.194
Overall	0.606	0.746	-46.270	<0.0001	0.187

Table 5. Interaction table from loglinear analysis of site, treatment, and functional group. df = degrees of freedom, partial chi-sq. = partial chi-square value.

Effect	df	Partial chi-sq.	*P*
Site	1	5.17	0.023
Treatment	3	6.25	0.100
Functional group	5	219.76	<0.001
Site*Treatment	3	27.81	<0.001
Site*Functional group	5	6.85	0.232
Treatment*Functional group	15	22.86	0.087
Site*Treatment*Functional group	15	24.91	0.051

Figure 1. Location of study sites – Zaleski State Forest and Raccoon Ecological Management Area – in Vinton County, Ohio.
Shading indicates presence of forest. Image modified from http://www.fs.fed.us/ne/delaware/4153/ffs/Ohio_Hills_Study_Site.htm.

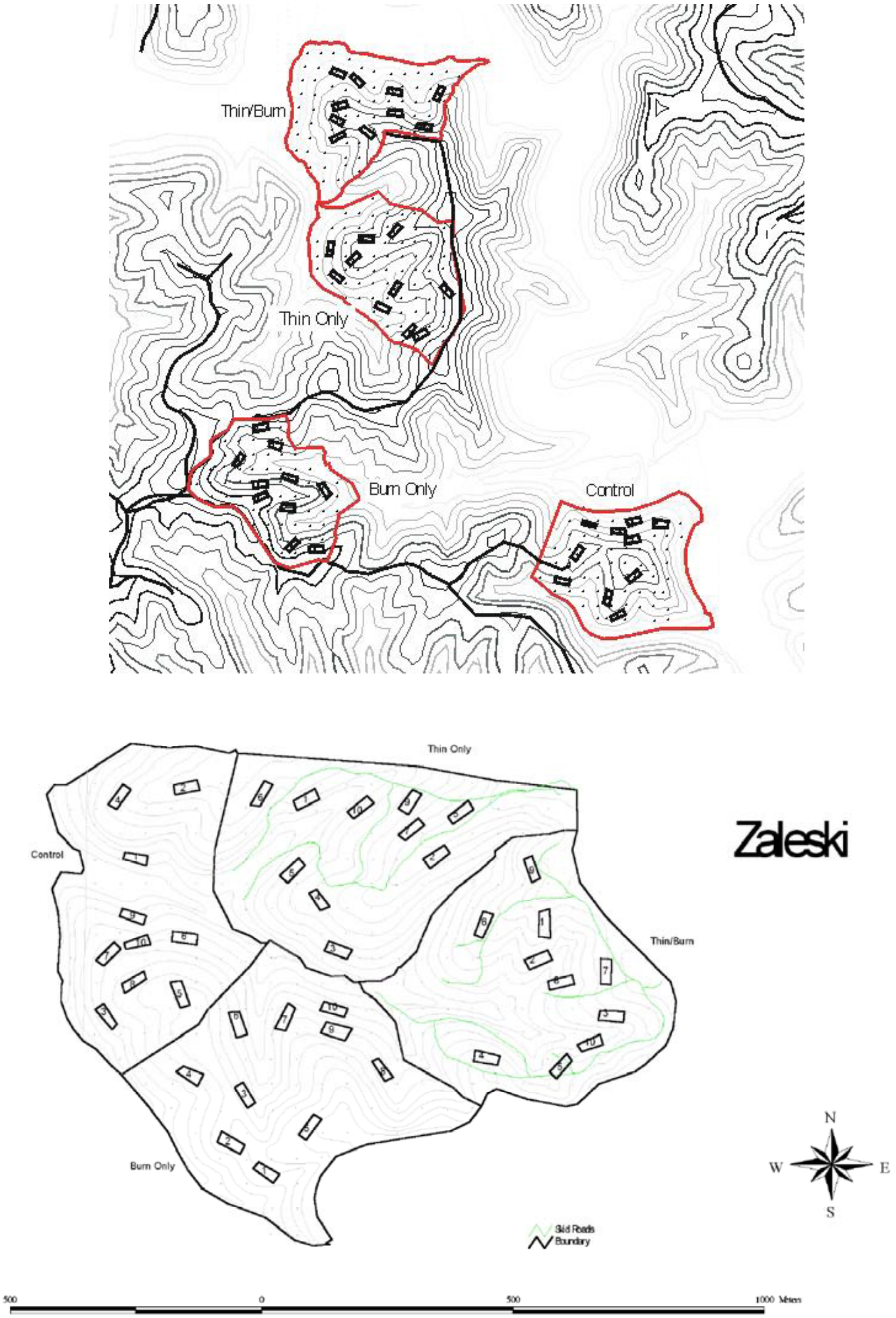

Figure 2. Relative location of experimental treatments and 20 × 50m permanent plots in each study area.
Upper map shows Raccoon Ecological Management Area, and lower map shows Zaleski State Forest. Images courtesy of http://www.fs.fed.us/ne/delaware/4153/ffs/maps.htm.

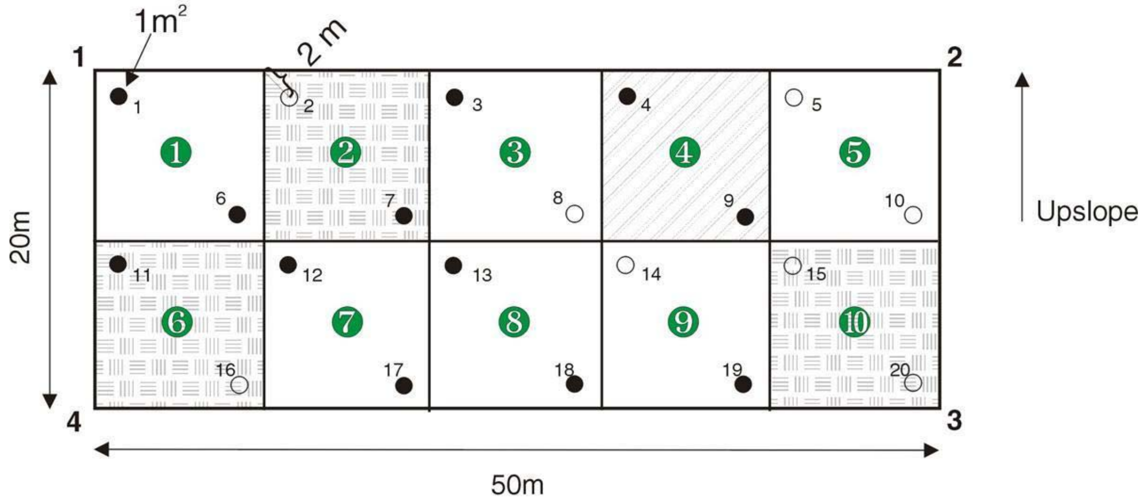

Figure 3. Layout of 20 × 50 m sampling plot.
Soil samples were collected in subplots 1, 4, 7, and 8, immediately outside the two circular vegetation plots. Image courtesy of http://www.fs.fed.us/ne/delaware/4153/ffs/plot_layout.htm.

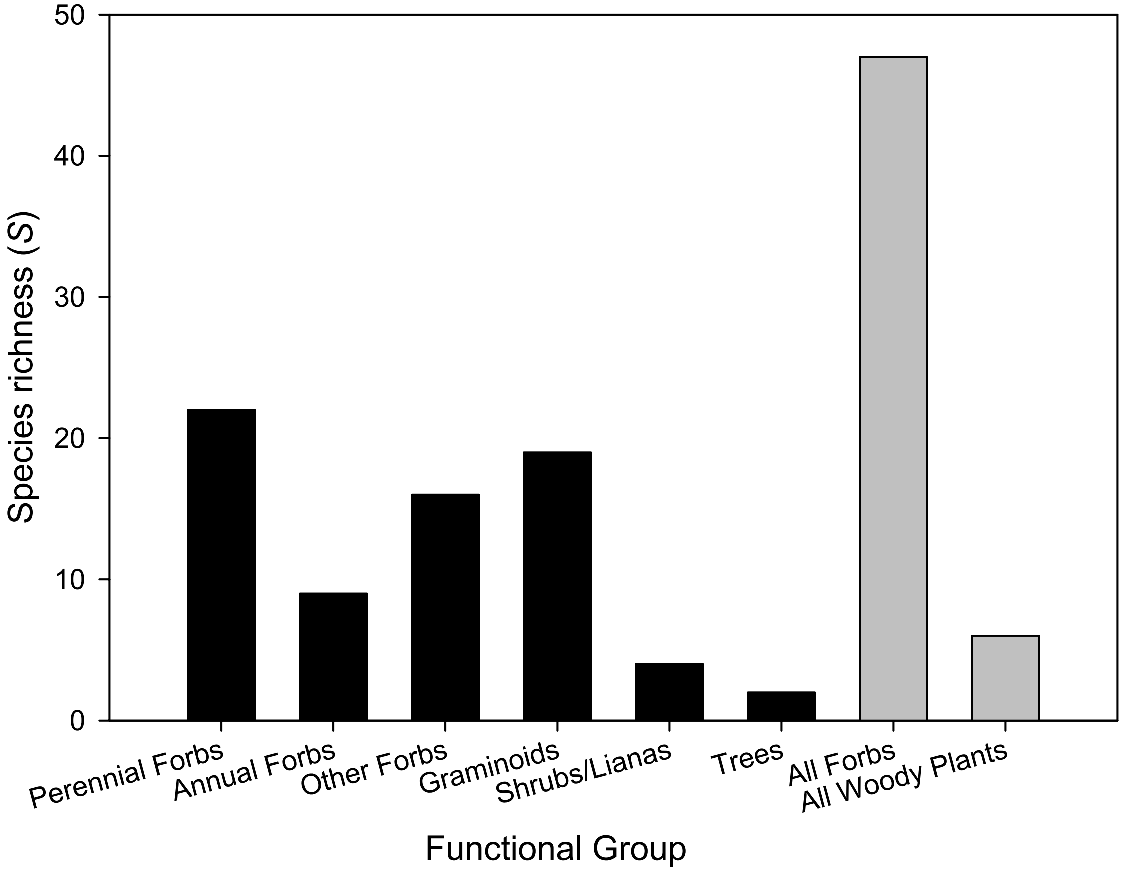

Figure 4. Number of species in each functional group category.
Other forbs includes unidentified species, and species that could not be determined to be annual or perennial. All forbs and all woody plants are included as summaries, but were not categories included in the loglinear analysis.

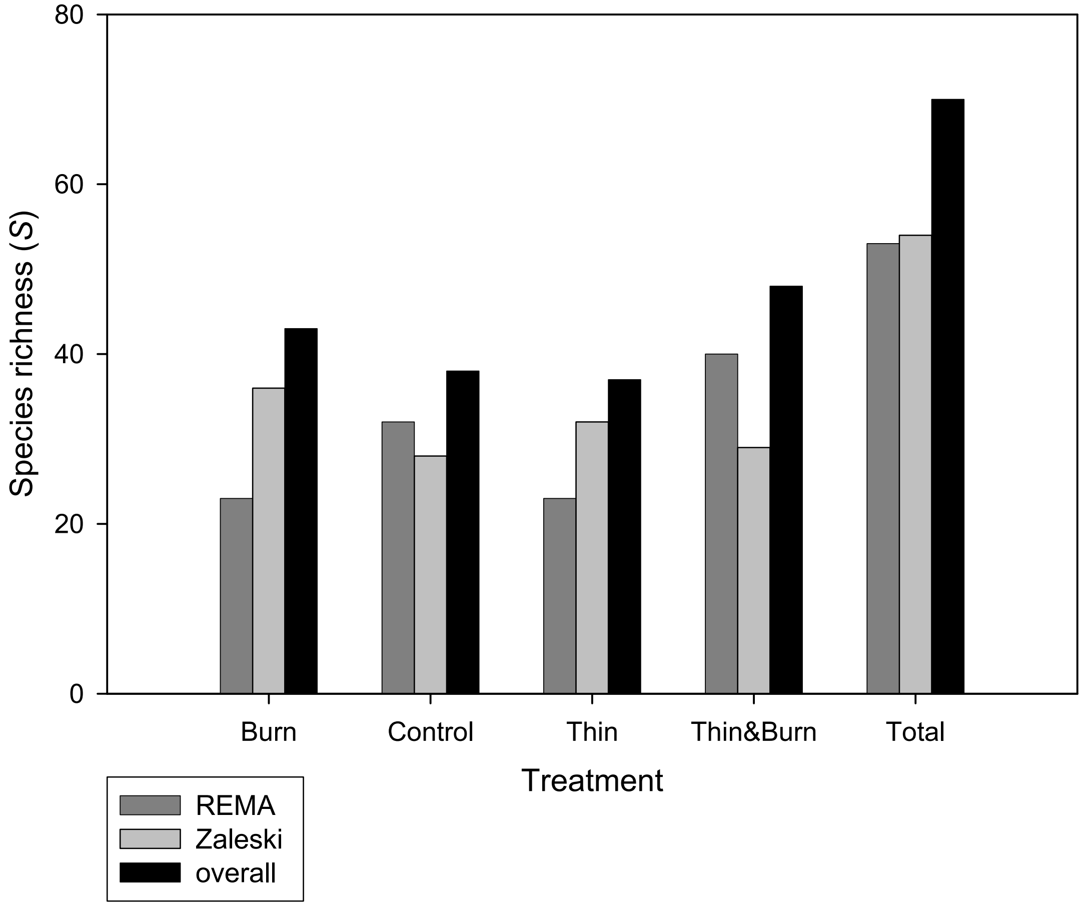

Figure 5. Species richness (*S*) values by treatment area and overall.

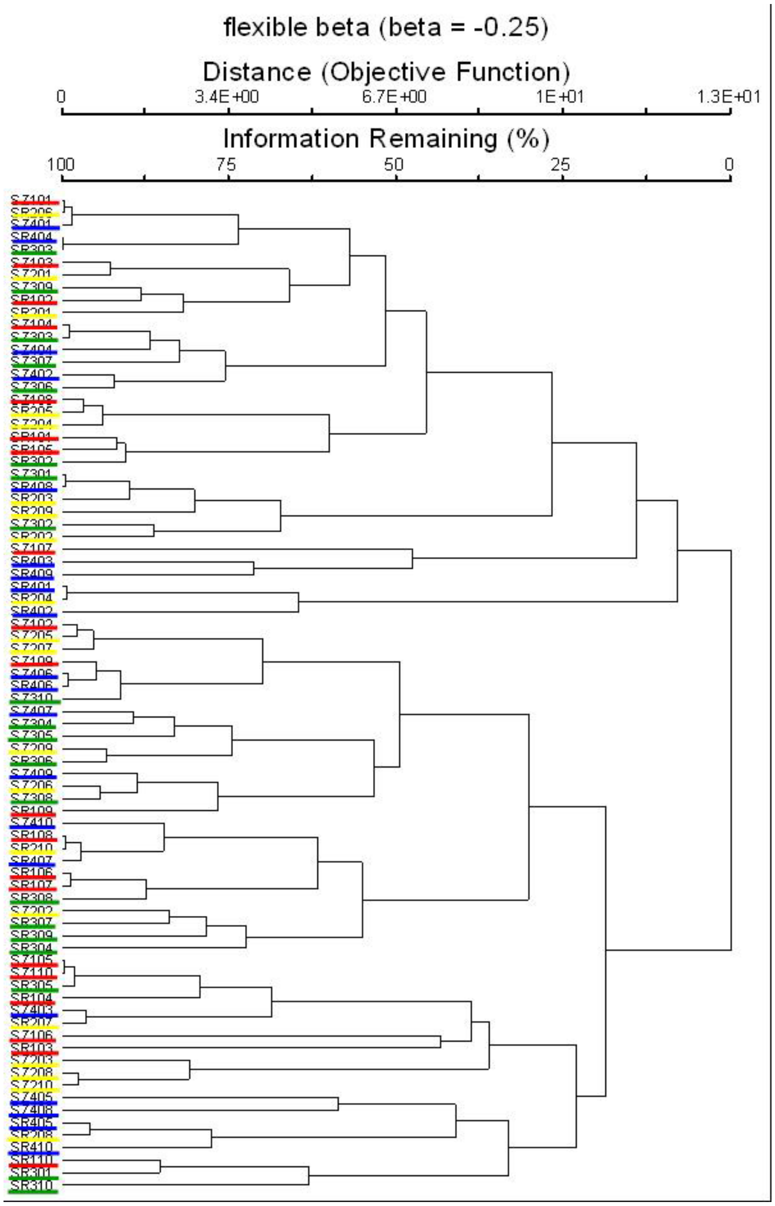

Figure 6. Cluster analysis of species composition of the 20 x 50m plots.
Cluster analysis of species composition of the 20 x 50m plots shows no clustering by treatment. Sørensen distance and flexible beta linkage method (β = -0.25) were used. Colors represent treatment units: Control, red; Thin, yellow; Thin & Burn, green, Burn, blue.

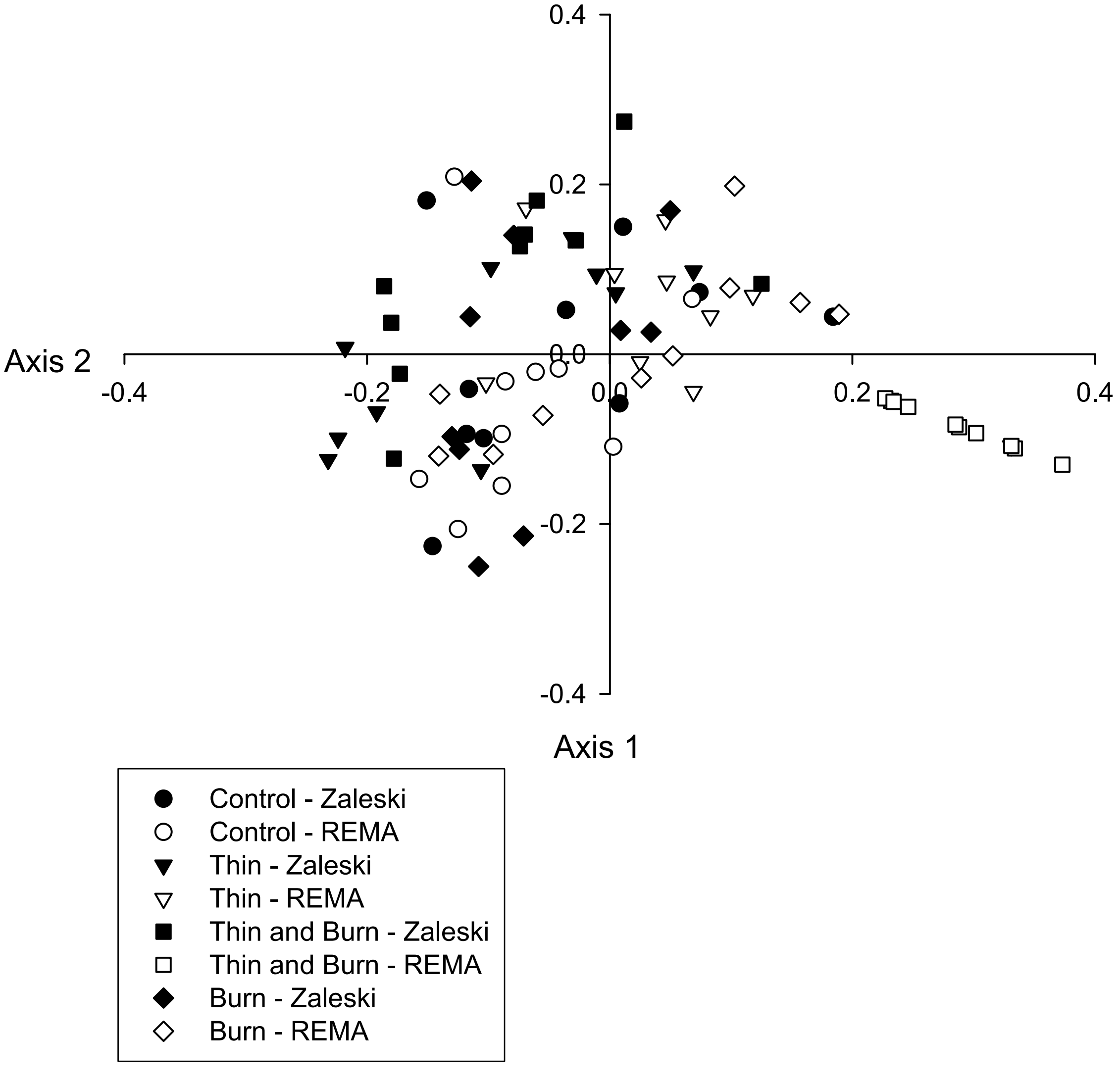

Figure 7. Principal coordinates analysis (PCO) of species composition in all treatments, showing Axes 1 and 2.

No separation between treatments is seen, but the Thin & Burn plots from REMA form a separate grouping off to the right.

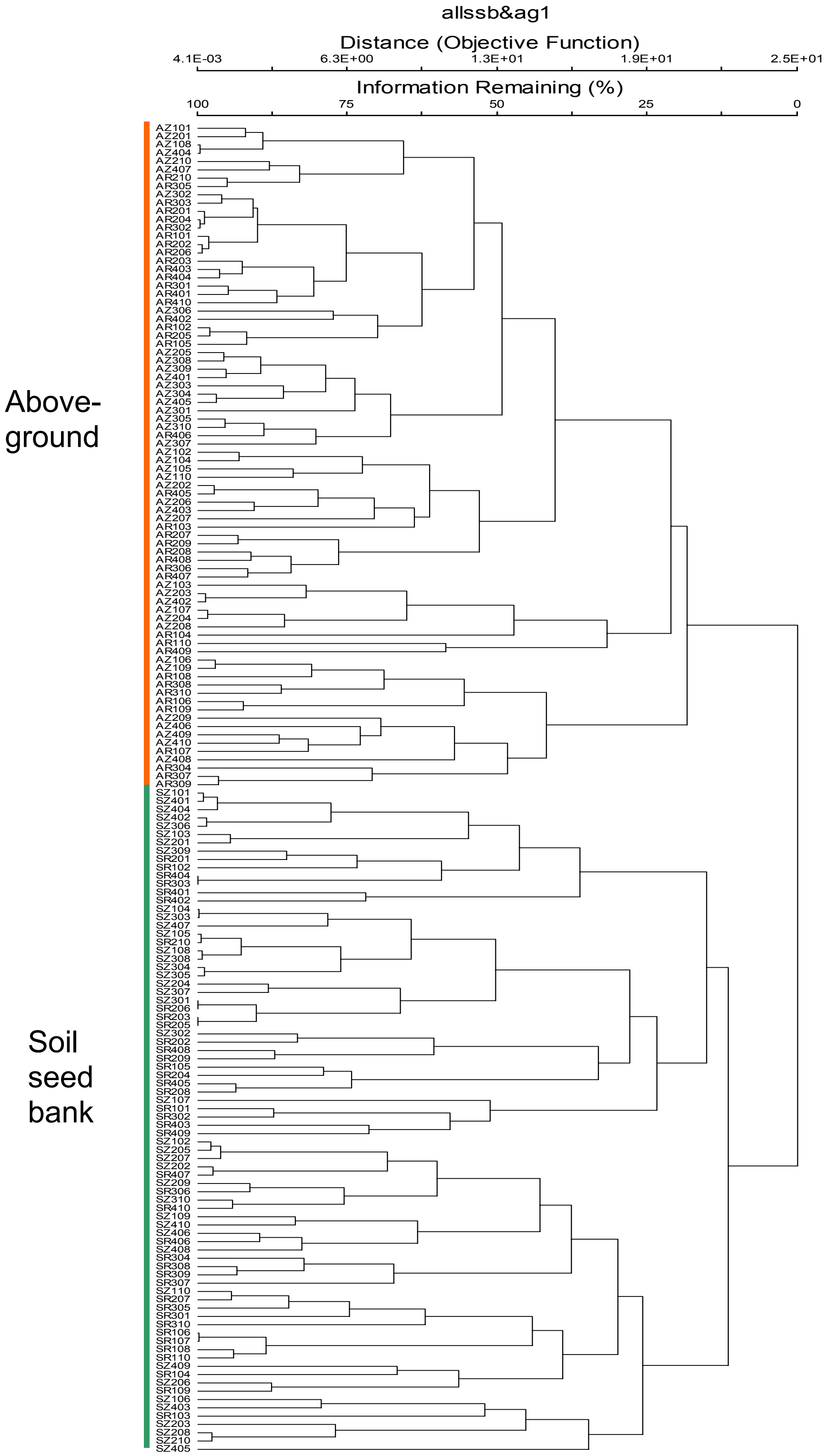

Figure 8. Cluster analysis showing separation of above-ground and soil seed bank plots, based on species composition.

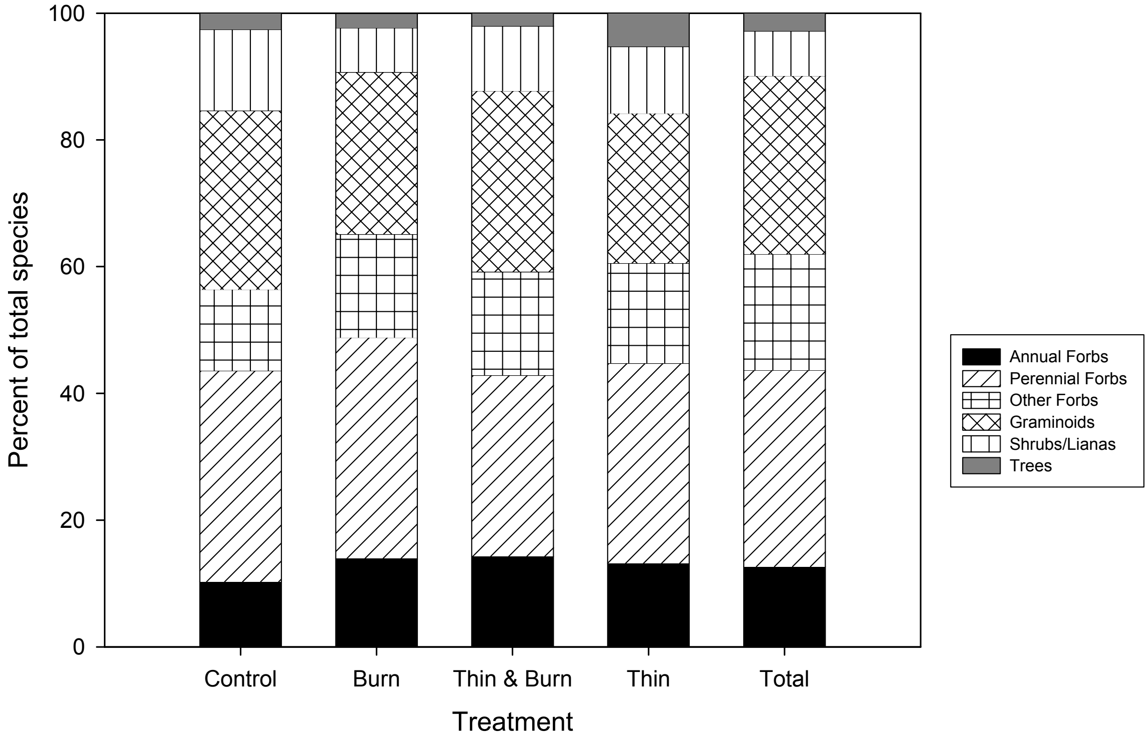

Figure 9. Stacked bar graph of percent of total species found in each functional group for each treatment.

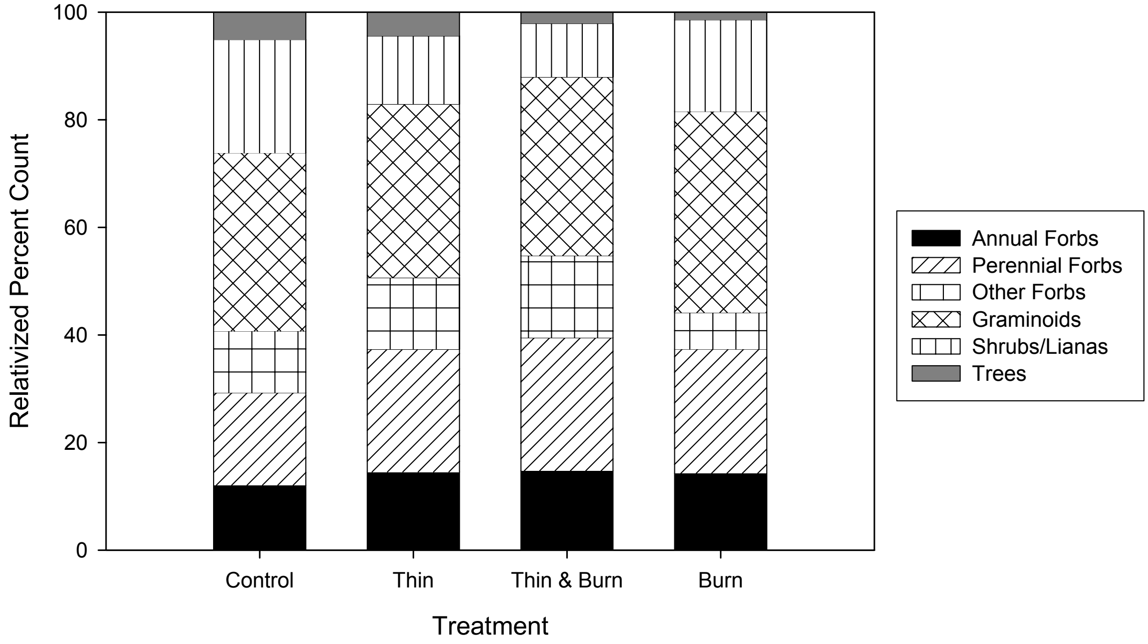

Figure 10. Stacked bar graph of relativized percent count of each functional group for each treatment.

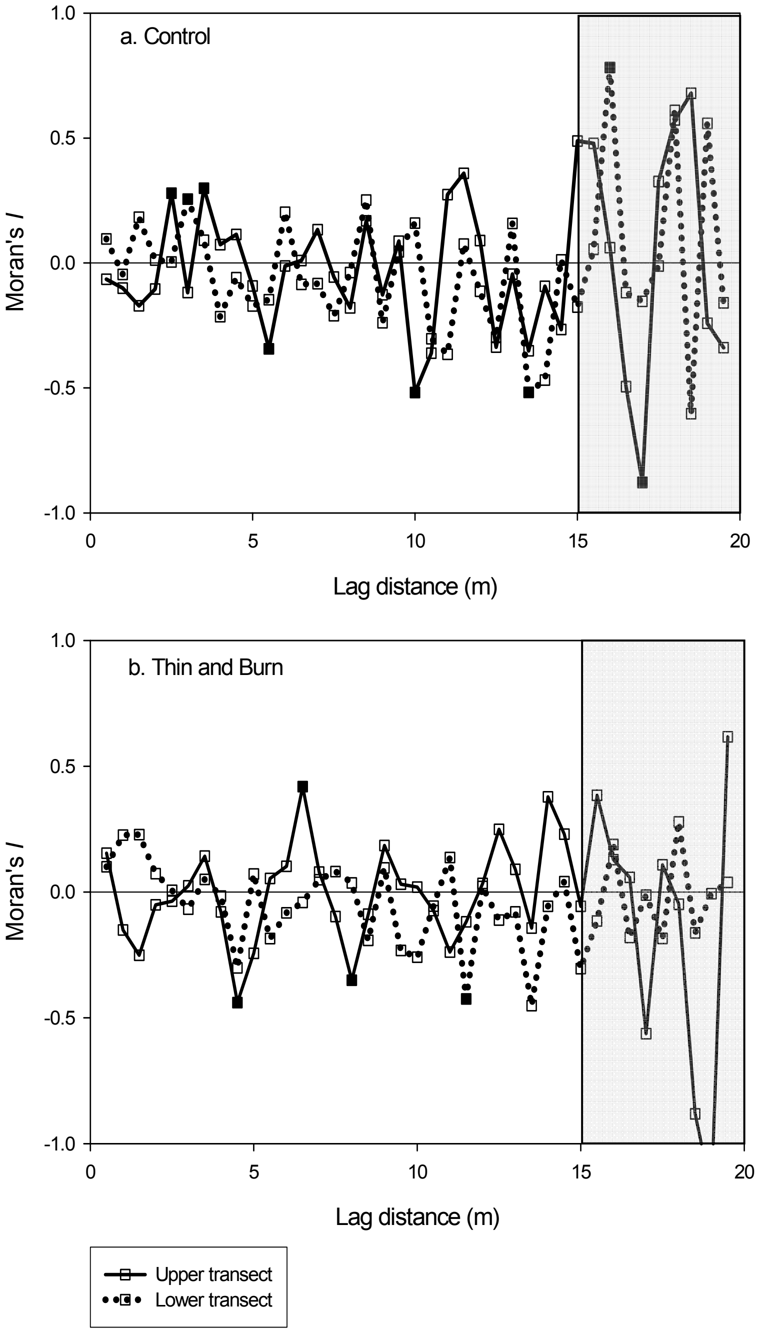

Figure 11. Moran's *I* correlograms for species richness values in Control and Thin & Burn units at Zaleski State Forest, Vinton County, Ohio.
Filled symbols indicate significant values ($P < 0.05$), based on Monte Carlo resampling (1000 permutations). Values in the shaded area are invalid, as they are based on too few pairs of samples.

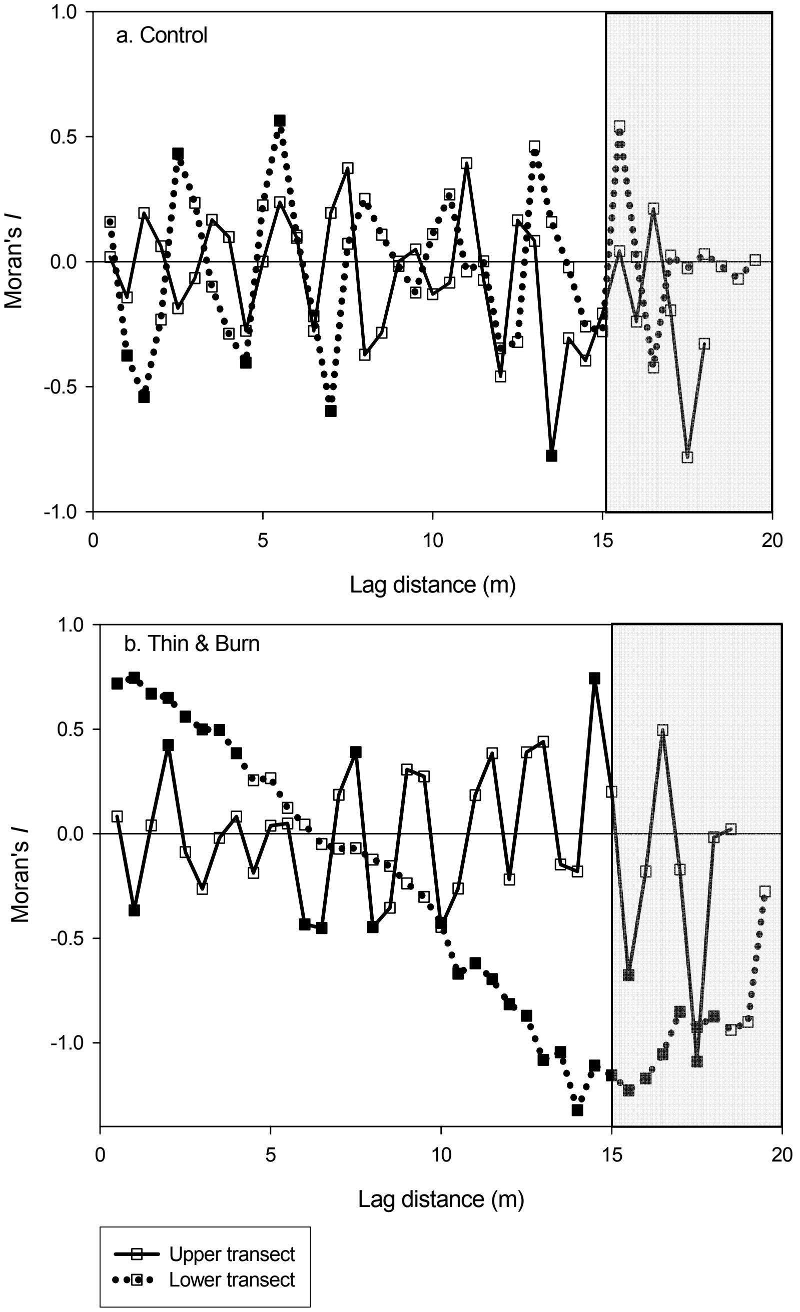

Figure 12. Moran's *I* correlograms for PCO values for Control and Thin & Burn units at Zaleski State Forest, Vinton County, Ohio.
Filled symbols indicate significant values ($P < 0.05$), based on Monte Carlo resampling (1000 permutations). Values in the shaded area are invalid, as they are based on too few pairs of samples.

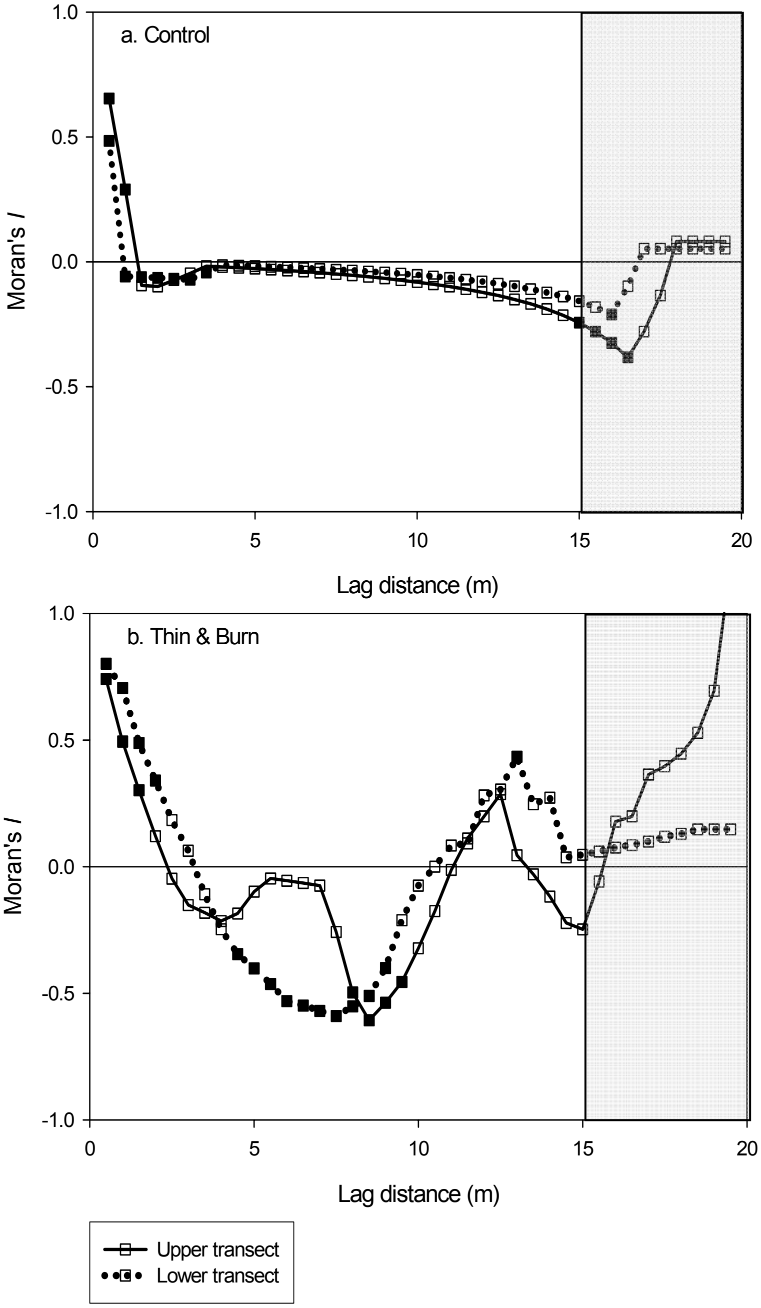

Figure 13. Moran's *I* correlograms for canopy cover along two transects in the Control and Thin & Burn units at Zaleski State Forest, Vinton County, Ohio.
Filled symbols indicate significant values ($P < 0.05$), based on Monte Carlo resampling (1000 permutations). Values in the shaded area are invalid, as they are based on too few pairs of samples.

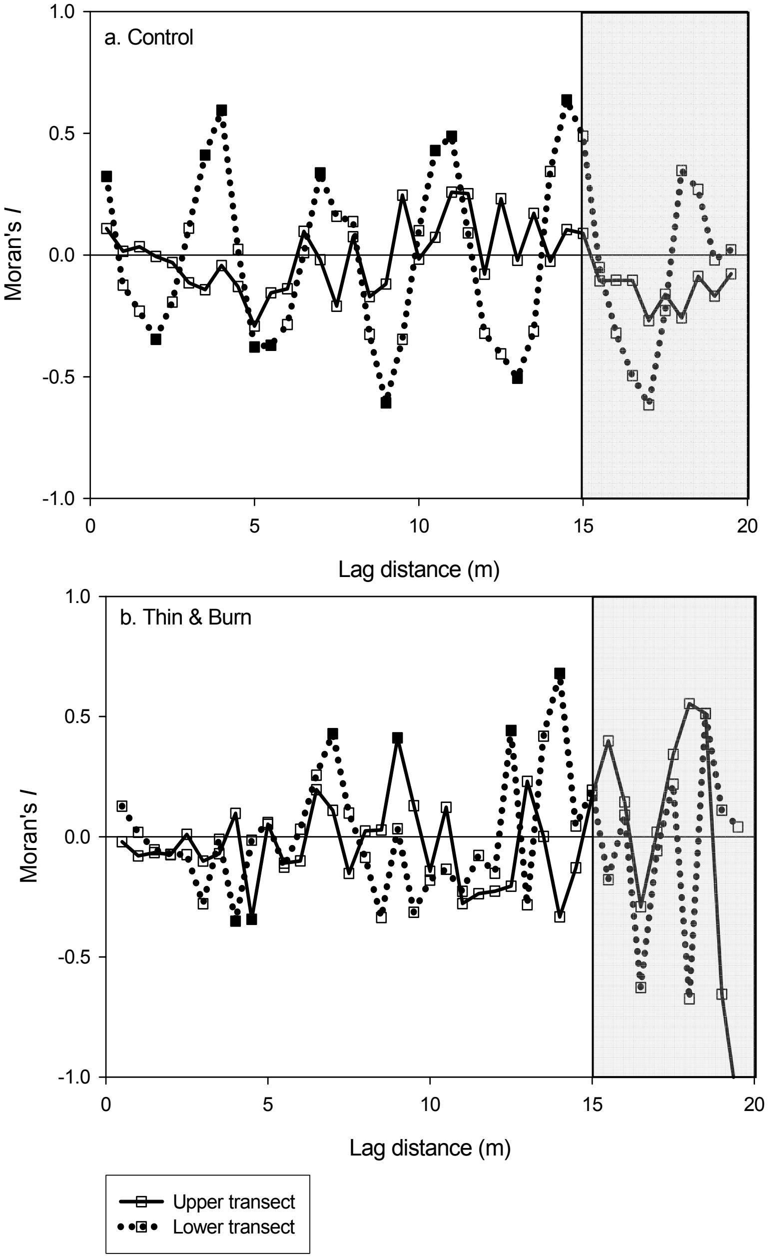

Figure 14. Moran's *I* correlograms for litter depth (cm) along two transects in the Control and Thin & Burn units at Zaleski State Forest, Vinton County, Ohio. Filled symbols indicate significant values ($P < 0.05$), based on Monte Carlo resampling (1000 permutations). Values in the shaded area are invalid, as they are based on too few pairs of samples.